
THE FOSSIL SNAKES OF PIT 91, RANCHO LA BREA, CALIFORNIA

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ABSTRACT. The known snake fauna from Rancho La Brea is increased from four species to 12 on the basis of material from recently reexcavated LACM 6909 (=Pit 91). Two taxa, *Masticophis lateralis* and the *Thamnophis couchii* group, are reported as fossils for the first time.

Recognition of intracolumnar vertebral position is necessary for identification. A previously undescribed feature, the subcentral lymphatic fossa, aids in determining vertebral position.

The composition of the fauna suggests that the locality represents a Pleistocene stream site traversing a prairie or scrub habitat. The fauna is similar to the modern Los Angeles region fauna. This common pattern among late Pleistocene herpetofaunas in North America contrasts with known endothermic faunas. It is suggested that the evolutionary stability of the North American herpetofauna, as compared with that of endotherms, may be due to an ability to maintain viable populations during periods of environmental stress that result in extirpation of endotherms.

INTRODUCTION

The most important late Pleistocene fossil vertebrate locality in North America is Rancho La Brea in Los Angeles, California. This site has produced thousands of fossils in a superb state of preservation and has provided one of the most detailed accounts of a late Pleistocene biological community known. Moreover, it is the type fauna for the Rancholabrean Provincial Land Mammal Age (Savage, 1951).

Rancho La Brea is located in the Los Angeles Basin within the city of Los Angeles. The fossil deposits overlie the Palos Verdes Sand, which is partly impregnated with asphalt at Rancho La Brea. Numerous accounts of dates and dating techniques for Rancho La Brea material have been published (Howard, 1960; Berger and Libby, 1966, 1968; Ho *et al.*, 1969; and McMenamin *et al.*, 1982). Estimates vary from about 4,000 to over 40,000 years B.P. (McMenamin *et al.*, 1982). See Stock (1956), Woodard and Marcus (1973), Shaw (1982), and Shaw and Quinn (1986) for detailed discussions of location, age, geology, stratigraphy, and history of excavation.

Early workers postulated that the tar deposits of Rancho La Brea represent previously fluid, viscous pools in which animals were trapped and entombed. These pools were conceived of as dynamic fluid bodies that underwent convective turnover that disarticulated skeletons, wore bone surfaces, and obliterated stratigraphy (Stock, 1956). Woodard and Marcus (1973) have shown that a gross stratigraphy exists in some pits and that some of

the material is entombed in stream deposits that were inundated by asphalt. Shaw and Quinn (1986) indicate that most animals were probably entrapped in thin sheets of tar exposed at the surface of the deposits.

Early studies of Rancho La Brea concentrated on its spectacular large mammal and avian faunas (see Stock, 1956, for a review and bibliography) but largely neglected vertebrate microfossils, invertebrates, microbotanical remains, taphonomy, and details of stratigraphy. In the 1940's, D.W. Pierce developed a technique for recovering minute fossils from the asphaltic matrix (Stock, 1956). Pierce's studies were mostly concerned with insect remains, but microvertebrate fossils were also recovered (Brattstrom, 1953b).

Brattstrom (1953b) published the first comprehensive treatment of amphibians and reptiles from Rancho La Brea, based partly on Pierce's collections. Snakes were poorly represented in this collection, and Brattstrom anticipated that greater diversity would be revealed by further collecting.

In 1969, a study was initiated at Rancho La Brea to improve understanding of aspects of the site that were not well documented by previous investigators. Locality LACM 6909 (=Pit 91), originally set aside for display purposes in 1915, is being reexcavated with careful attention to taphonomy, the recovery of microfossils, stratigraphy, etc. (Shaw, 1982; Shaw and Quinn, 1986). Lower levels of this deposit are partly composed of natural stream sediments that may yield some stratigraphic information. Radiocarbon dates on wood and bone collagen from Pit 91 range from 25,100 to over 40,000 years B.P. (Marcus and Berger, 1984), revealing that Pit 91 is relatively old among Rancho La Brea deposits. The present study is based on the snake

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remains from this excavation and documents the diversity that Brattstrom (1953b) anticipated.

OPHIDIAN OSTEOLOGY

Fossilized snake remains are relatively common in Neogene deposits that bear vertebrates. The most important factor contributing to their abundance is probably the large number of skeletal elements per individual. The number of precaudal body segments in snakes typically ranges between 150 and 300. Each of these segments bears three skeletal elements, a vertebra and two ribs. Because of their fragile nature, the ribs and many skull elements are not commonly found as fossils. Other factors affecting the number of snake remains in the fossil record are the relative abundance of individuals in fossil communities and the durability of their solidly constructed vertebrae (Holman, 1981). Articulated snake skeletons are rare in the fossil record. Most snake remains are found in stream deposits and predator accumulated deposits. For these reasons, isolated vertebrae are by far the most frequently encountered and closely studied snake fossils.

A general guideline for identifying North American Pleistocene snakes is presented by Holman (1981, appendix). Auffenberg (1963), Brattstrom (1967), and Meylan (1982) also treat this topic. Identification of snake skeletal elements to genus or species depends on recognition of ranges of variability of subtle characters and proportions and requires the use of extensive comparative collections (Holman, 1981). Identification is usually simplified by limiting comparisons of Pleistocene fossils to living taxa from a limited geographic area.

The difficulties involved in vertebral identification have been widely recognized, and the practice is often viewed with skepticism because of numerous factors that contribute to the variability of vertebral morphology, not only between taxa but within taxa. Individuals vary both ontogenetically and topographically along the vertebral column. Morphological features change gradually from one character state to another as one proceeds down the vertebral column. In most instances this change is imperceptible in consecutive vertebrae. Furthermore, similar character states may appear in different regions of the vertebral column in different taxa. These factors encumber qualitative description and often force one to rely on comparative terms, using one species as a standard for another. Given ample time and comparative material, however, recognizable patterns in vertebral morphology emerge. Unfortunately, extensive comparative collections are relatively few, and their geographic and ontogenetic representation are often limited.

Some authors have relied on qualitative methods of discrimination to identify snake vertebrae. Others have used ratios of linear measurements as size free discriminators. The use of ratios originated with Auffenberg (1963) and has been continued by

Van Devender *et al.* (1977, 1985), Van Devender and Worthington (1977), Van Devender and Mead (1978), and Mead *et al.* (1984). Meylan (1982) has gone a step further by using discriminant analysis to distinguish taxa using populations of ratios of linear measurements.

Although the use of quantitative analysis in conjunction with qualitative characters would be beneficial, most previous workers (using quantitative or qualitative methods) have relied exclusively on the use of mid-trunk vertebrae to identify fossils, while providing little information on how these are distinguished from vertebrae of other regions of the vertebral column. This is unfortunate because, for many characters, the novice may confuse vertebrae from one region of the column of one species with those from a different region in other species. Furthermore, the use of ratios as statistical discriminators has been criticized (Atchley *et al.*, 1976). Unfortunately, quantitative comparisons of characters spanning the entire vertebral column in even a single extant snake species are very few and limited in scope (e.g., Hoffstetter and Gayard, 1965). The present study relies almost entirely on qualitative comparison.

Although the descriptions of the criteria for identifying snake vertebrae are admittedly cumbersome, qualitative techniques remain the only readily accessible approach to the gross study of entire ophidian paleofaunas. However, taxonomic refinement of fossil snakes will require quantitative study of interspecific, intraspecific, and ontogenetic shape variation in the vertebrae of living and fossil taxa.

DESCRIPTIVE TERMINOLOGY

Auffenberg (1963) provided descriptive terminology for shape variation in snake vertebrae that most subsequent authors have followed. New descriptive terms introduced here require some clarification. Most of these terms refer to shapes of structures and derive from a simple division of shape characters into extremes and intermediates, e.g., elongate, shortened, moderately elongate, etc. In an attempt to provide a quantitative characterization for these shape descriptors, limits for the character states were defined by choosing borderline cases and calculating ratios for measurements of features that strongly affect the shape. The average of these ratios provided approximate limits for character states. Individual fossils were matched with a taxon by visual comparison of these character states. Abbreviations follow Auffenberg (1963) or are described below. Measurements used in this study are illustrated in Figure 1.

Vertebral Length. In this paper, a vertebra is considered *elongate* if CL/NAW (centrum length to neural arch width) is approximately 1.2 or greater (Fig. 1). If 0.8 or less, the vertebra will be considered *short* or *broad* (Fig. 2A). Intermediate values will be referred to as *moderately elongate* (Fig. 5B).

Zygapophyses. These are *produced laterally* if

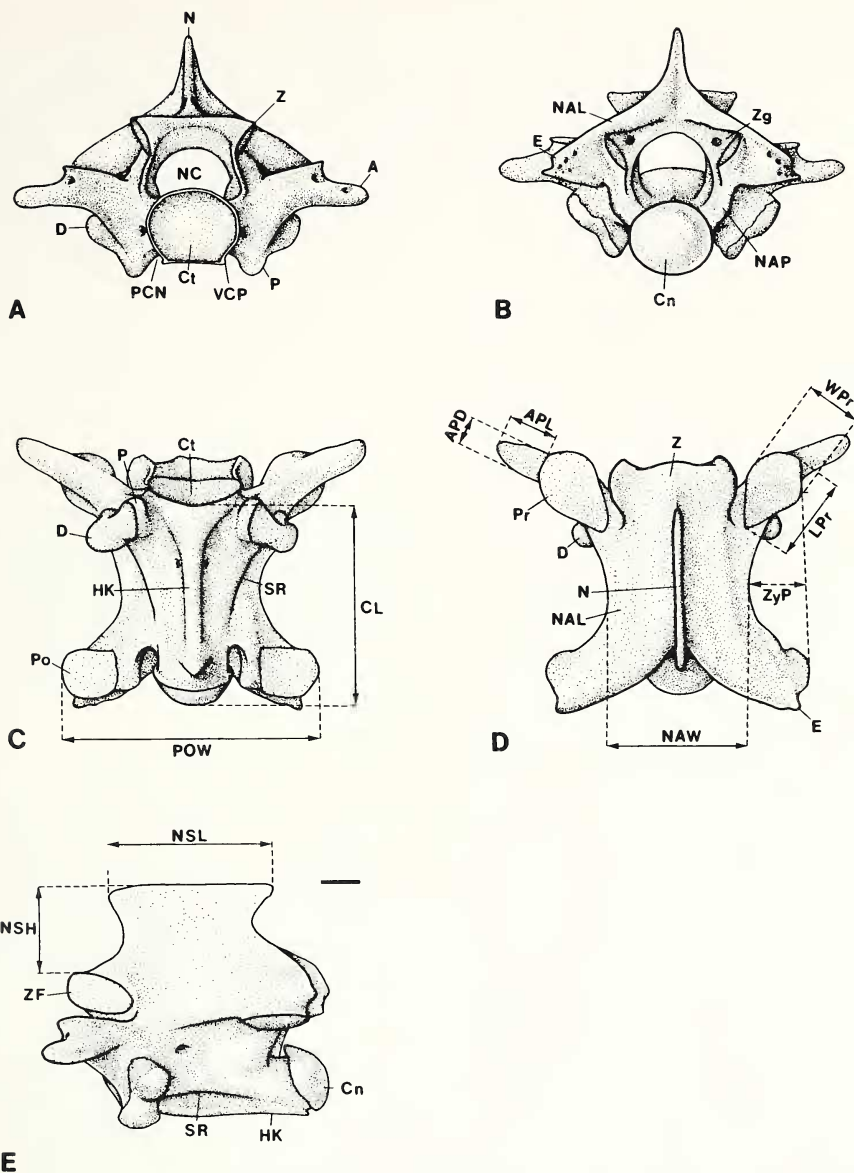


Figure 1. MTV of *Coluber constrictor*, illustrating anatomical terms and measurements used in text. A. Anterior view. B. Posterior view. C. Ventral view. D. Dorsal view. E. Lateral view. Abbreviations: A = accessory process, APD = accessory process diameter, APL = accessory process length, CL = centrum length, Ct = cotyle, Cn = condyle, D = diapophysis, E = epizygapophyseal spine, HK = hemal keel, LPr = length of prezygapophysis, N = neural spine, NAL = neural arch lamina, NAP = neural arch pedicel, NAW = neural arch width, NC = neural canal, NSH = neural spine height, NSL = neural spine length, P = parapophysis, PCN = paracotylar notch, Po = postzygapophyseal facet, POW = width across postzygapophyses, Pr = prezygapophyseal facet, SR = subcentral ridge, VCP = ventrolateral cotylar process, WPr = width of prezygapophysis, Z = zygosphene, ZF = zygosphenal facet, ZG = zygantrum, ZYP = greatest distance between a lateral tangent to zygapophyses and neural arch. Bar = 1 mm.

the ratio between the greatest distance from a lateral tangent of the zygapophyseal facets to the neural arch (ZyP, Fig. 1D) and CL is 0.40 or greater (Fig. 2A). If less than 0.33, the zygapophyses are *not produced laterally* (Fig. 2B). Intermediate values are moderately produced.

Neural Arch Laminae. These may be either *straight* (Fig. 2E), *convex* (Fig. 2C, 8A), or *convex laterally* (Fig. 2D) in posterior view.

Neural Spine. If the anterior height of this structure (NSH) is approximately half its dorsal length (NSL), then it is considered of *medium height* (Fig.

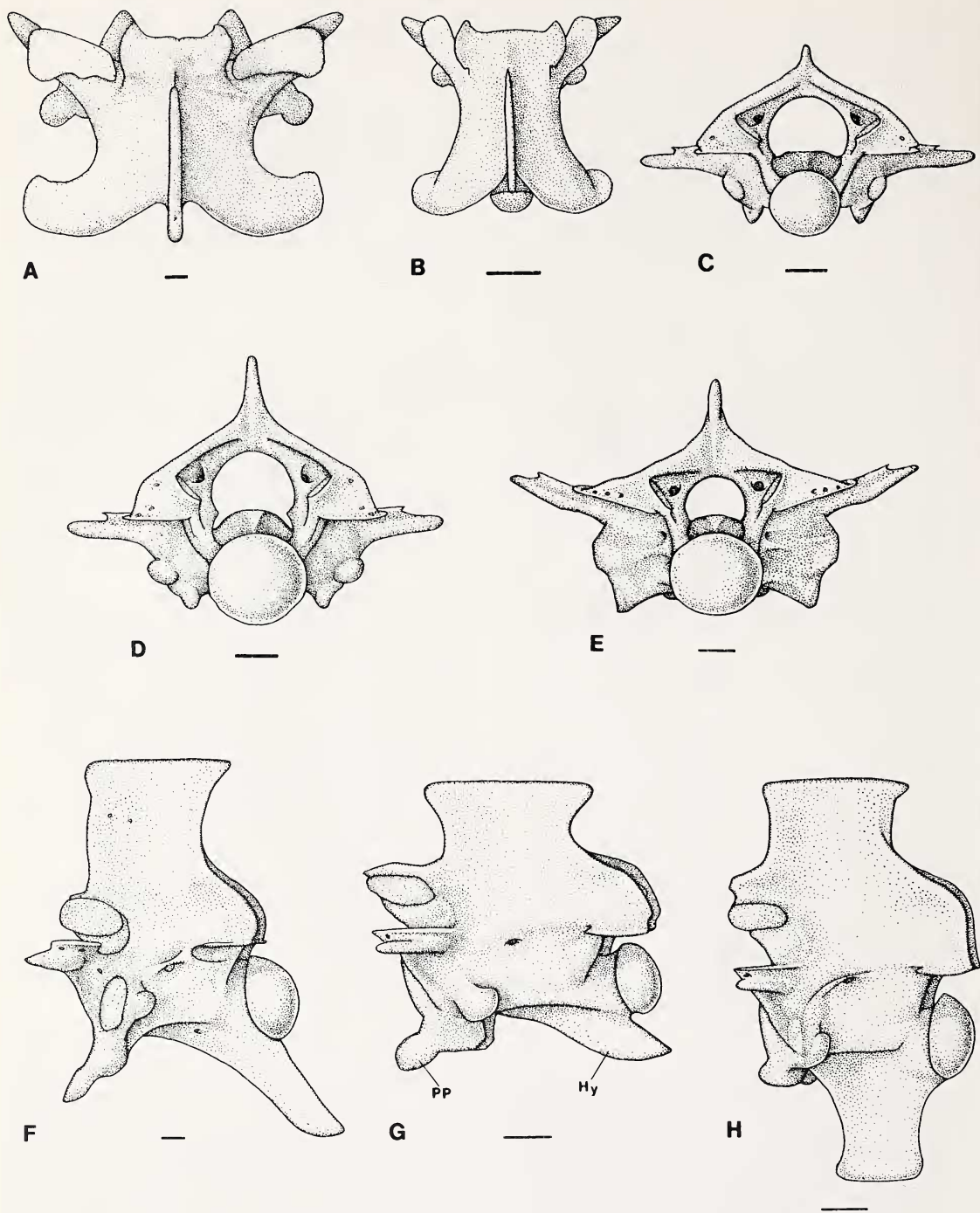


Figure 2. Examples of character states used to describe vertebrae, taken from modern comparative specimens. **A.** Dorsal view of MTV of *Agkistrodon piscivorus*, illustrating zygapophyses produced laterally. **B.** Dorsal view of ATV of *Drymobius margaritiferus*, illustrating nondivergent zygapophyses. **C.** Posterior view of MTV of *Coluber constrictor*, illustrating a moderately vaulted neural arch with convex laminae. **D.** Posterior view of MTV of *Arizona elegans*, illustrating a moderately vaulted neural arch with laterally convex laminae. **E.** Posterior view of MTV of *Heterodon platyrhinos*, illustrating a depressed neural arch with flat laminae. **F.** Lateral view of *Agkistrodon piscivorus* MTV showing a spine-like hypapophysis. **G.** Lateral view of MTV of *Thamnophis sirtalis*, showing a short, blade-like hypapophysis with a sinuous anteroventral border. **H.** Lateral view of ATV of *Pituophis melanoleucus*, showing a ventrally directed, blade-like hypapophysis, which is squared distally. Abbreviations: Hy = hypapophysis, PP = parapophyseal process. Bar = 1 mm.

2G). If the anterior height is distinctly less than this, it is referred to as *low*. If distinctly greater, it is referred to as *tall* or *high* (Fig. 2F).

Accessory Processes. If the diameter perpendicular to the long axis of this structure (APD) is less than half the greatest width of the prezygapophysis (WPr), they are referred to as *thin* (Fig. 1D). If APD is greater than half, they are referred to as *thick* (Fig. 13A). If the accessory process length (APL) is about half as long or longer than the greatest length of the prezygapophysis (LPr), it is termed *long* (Fig. 1D). If less than this, it is of *medium length* or *short* (Fig. 4B, 4A). The distal end may be *rounded* (Fig. 1D, 13A) or *pointed* (Fig. 4B).

Hypapophysis. The hypapophysis may be *spine-like* (Fig. 2F) (i.e., a cross section perpendicular to its long axis is about as long as wide or slightly longer) or *blade-like* (Fig. 2G), in which case the cross section is considerably longer than wide (as in most natricines). The distal tip of the hypapophysis may be *pointed* (Fig. 2G) or *squared off* (Fig. 2H, 5A). The anterior edge may be *simple* or *straight*, in which case it sweeps back gently to meet the posterior edge (Fig. 2F), or it may be *sinuous*, if its anteroventral border is strongly convex or angular (Fig. 2G).

VERTEBRAL REGIONS

There has been little agreement on how one should refer to the regions of the vertebral column of snakes. Although various authors have used the terms cervical, thoracic, and lumbar (Sood, 1948; Bullock and Tanner, 1966; Brummer, 1980; Szyndlar, 1984), this is clearly improper when applied to snakes because there is no way to determine the homology of snake vertebral regions with those of mammals, for which this terminology was devised (Romer, 1956). Even attempts to compare snake vertebral regions with those of lizards have been unsuccessful (Hoffstetter and Gasc, 1969) because of the variable and gradual nature of the dissociation of limb girdles from the vertebral column in series of lizard taxa with progressive degrees of limb reduction. Homology is further obscured by our general ignorance of the mechanisms by which body segments proliferate phylogenetically in tetrapod taxa.

The terminology of Hoffstetter and Gasc (1969) is the most useful in referring to snake vertebral regions. They specify four general regions.

- 1) Atlas and axis. These are unique and readily distinguished as in most tetrapods.
- 2) Trunk vertebrae (Fig. 1, 2). These are generalized vertebrae that lack the processes that distinguish the following regions. Hypapophyses (Fig. 2F, 2G, 2H) are always present anteriorly and may be present posteriorly.
- 3) Cloacal vertebrae (Fig. 3A, 3B). This region is distinguished by the presence of fused lymphapophyses, hemapophyses may also be present.

- 4) Postcloacal vertebrae (Fig. 3C, 3D). This and the cloacal region comprise the caudal series of most authors. The postcloacal region is characterized by absence of lymphapophyses and presence of pleurapophyses and hemapophyses.

These regions are readily distinguished, with at most one vertebra with intermediate conditions between regions 2 and 3, and 3 and 4.

The terminology of Hoffstetter and Gasc (1969) does not recognize subregions of the trunk, although a considerable degree of regular but less abrupt morphological change occurs. Assignment of vertebrae to a subregion of the trunk region is helpful and may be crucial to proper identification of isolated vertebrae. In this study, one minor and three major subregions of the trunk are distinguished. These subregions merge gradually into one another, with extensive areas of intermediacy. Assigning isolated vertebrae to subregions is not always clear-cut and is only intended as an aid to identification. Intermediate forms were arbitrarily assigned to one of two adjacent subregions.

The following detailed description of morphological changes between subregions serves as a guide to determine the extent of each subregion in a complete skeleton. These features are best seen in disarticulated specimens in which vertebral order has been preserved. The proportion of the vertebral column occupied by each region varies among taxa. The descriptions are based largely on observations of North American caenophidians and may not apply to other infraorders or caenophidians from other geographic regions. Figures 4–8 illustrate the features described below as seen in representative vertebrae of the three major subregions (ATV, MTV, and PTV below) from a single specimen.

Anterior Trunk Vertebrae (ATV; Fig. 4A, 5A, . . . , 8A). This region excludes the atlas and axis. ATV bear hypapophyses in all snakes examined. The anterior-most vertebrae (not illustrated) are shortened craniocaudally. The zygapophyses are small and are not produced laterally. Zygapophyseal facets are elongate craniocaudally in the first few vertebrae but quickly become rounded. The neural canal is relatively large in this region and has strongly convex laminae. The zygosphenes are broad. Parapophyseal processes are large, projecting cranioventrally. Neural spines are moderately high and thin. Hypapophyses are thin and point caudally in the first few vertebrae but quickly become stout, directed ventrally or posteroventrally, and may be squared off distally.

Proceeding caudally through the ATV region (Fig. 4A, 5A, . . . , 8A), overall vertebral size and relative vertebral length gradually increase. Zygapophyses increase in size and extend farther laterally. The neural canal becomes relatively smaller as the vertebrae become larger. The zygosphenes become relatively narrower, and parapophyseal processes decrease slightly. The neural spine often assumes its

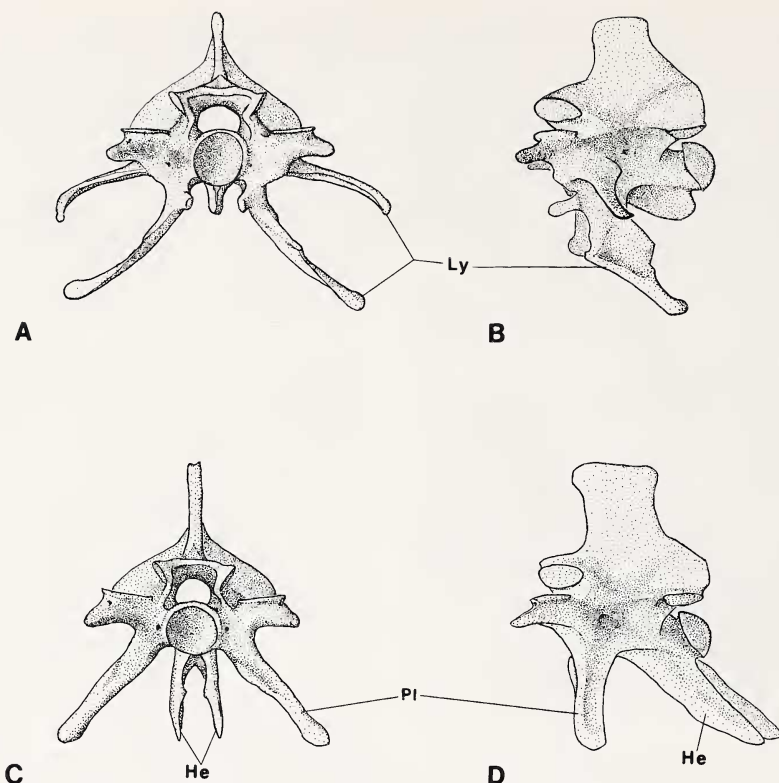


Figure 3. Caudal vertebrae of *Nerodia sipedon*. **A.** Anterior view of cloacal vertebra. **B.** Lateral view of cloacal vertebra. **C.** Anterior view of postcloacal vertebra. **D.** Lateral view of postcloacal vertebra. Abbreviations: He = hemapophyses, Ly = lymphapophyses, Pl = pleurapophyses. Bar = 1 mm.

greatest height at the caudal end of this region. Hypapophyses remain approximately the same length throughout most of the region or decrease only slightly posteriorly. In forms that lack mid-trunk vertebral (MTV) hypapophyses, hypapophyseal length decreases rapidly over four to six vertebrae in the zone of transition to MTV.

The caudal end of this zone is readily identified in forms that lack MTV hypapophyses as the point where hypapophyses are no longer distinguishable. In forms that have MTV hypapophyses, the transition from ATV to MTV zones is more subtle but can be detected by relying on the other characters discussed below.

Mid-trunk Vertebrae (MTV; Fig. 4B, 5B, . . . , 8B). These are the largest vertebrae and are the only ones used in identification of fossils by many authors. They become slightly more elongate posteriorly from the cranial to the caudal end of the region. Zygopophyses are produced farthest laterally in this region. The neural canal becomes relatively smaller throughout the rest of the length of the vertebral column. The zygosphenes remain approximately the same relative width as the caudal-

most ATV throughout this region. Parapophyseal processes are absent in this and following regions in forms that lack posterior hypapophyses. Where posterior hypapophyses are present, parapophyseal processes remain strongly developed throughout (see also Malnate, 1972). Hypapophyses are generally directed caudally and may be somewhat pointed, never squared off. A slight decrease in relative hypapophysis length may occur throughout this and the next region. Neural spines generally decrease in relative height slowly throughout this and the next vertebral regions.

The transition from this zone to the next is always extensive and subtle, but cranial MTV and caudal posterior trunk vertebrae (PTV) from the same individual are always readily distinguishable.

Posterior Trunk Vertebrae (PTV; Fig. 4C, 5C, . . . , 8C). This region has not been distinguished from the MTV in the literature, and it is impossible to tell from published accounts whether PTV have been considered while making identifications. In some species, features that have been considered diagnostic in trunk vertebrae (e.g., neural spine height) have been found to differ in these two

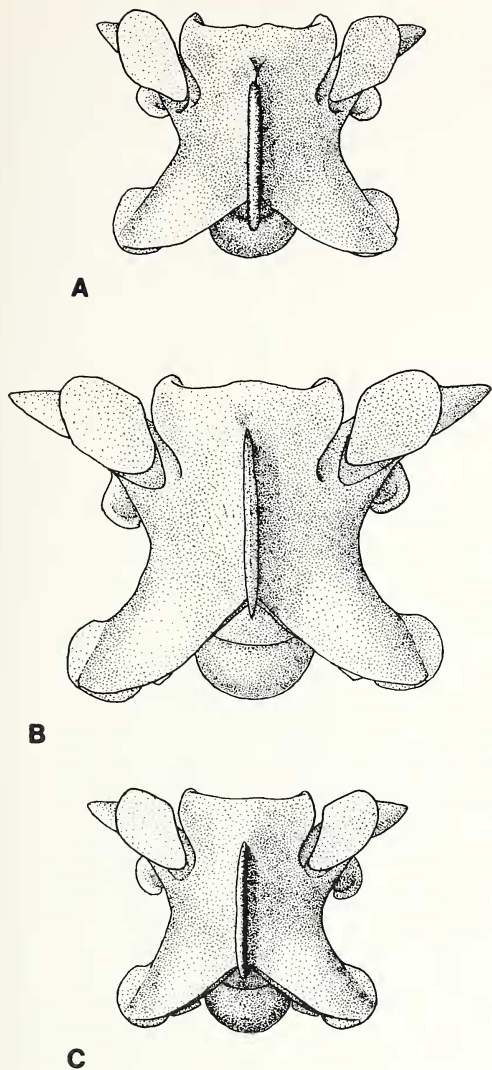


Figure 4. Comparison of the dorsal aspects of three vertebrae from a single specimen of *Pituophis melanoleucus sayi*, a male (snout-vent length 1,039 mm) with 222 precaudal vertebrae, showing changes in shape within a single vertebral column. A. ATV (20th vertebra). B. MTV (85th vertebra). C. PTV (210th vertebra). Bar = 1 mm.

regions, such that PTV of one species may be more similar to MTV of a second species than to their own MTV in this character. For example, *Crotalus horridus* Linnaeus, 1758 is said to be distinguishable from *C. adamanteus* (Beauvois, 1799) (as well as many other *Crotalus* species) by its low neural spines (Auffenberg, 1963; Holman, 1967). However, the neural spines of the PTV of *C. adamanteus* may be fully as low as those of the MTV of *C. horridus*. Many similar examples could be cited using other characters and taxa.

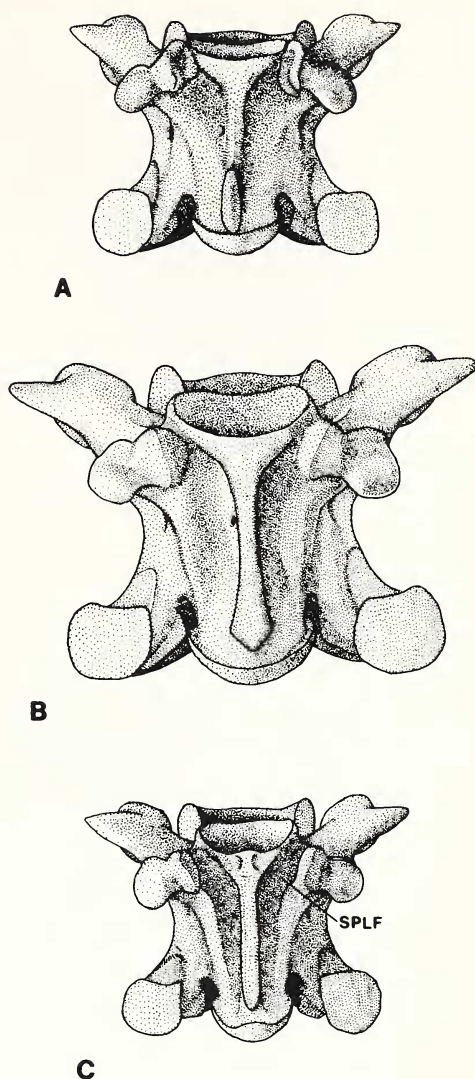


Figure 5. Comparison of the ventral aspects of the three vertebrae illustrated in Figure 4. Abbreviations: SPLF = subcentral paramedian lymphatic fossa. Bar = 1 mm.

The most distinctive aspect of the PTV is a pair of subcentral paramedian lymphatic fossae (Fig. 5C, 13A). This feature has previously received very little attention. Brummer (1980) referred to these fossae as subcentral pits, whereas Hill (1971) called them subcentral excavations. Neither of these authors made any reference to the cause of these structures. Other authors (Auffenberg, 1963; Meylan, 1982) have attributed them to extreme development of the subcentral ridges on otherwise normal centra. This is clearly not the case because these fossae are incised to a level that is well dorsal to the normal level of the ventral face of the centrum with respect to the ventral edges of the cotyle and condyle.

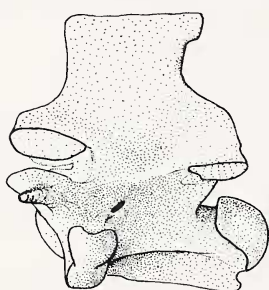
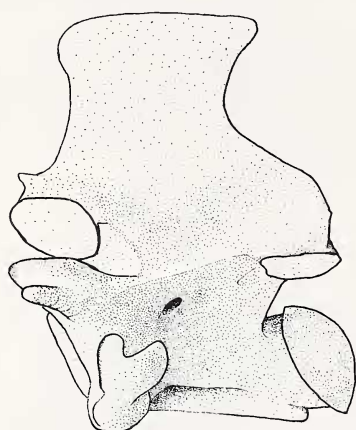
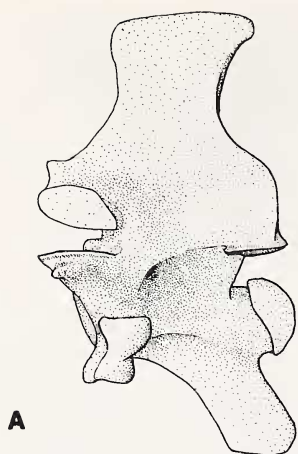


Figure 6. Comparison of the left lateral aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

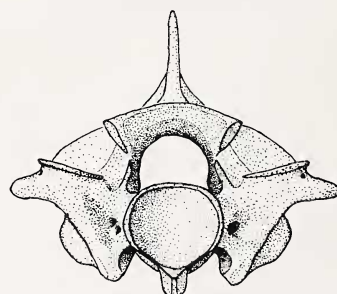
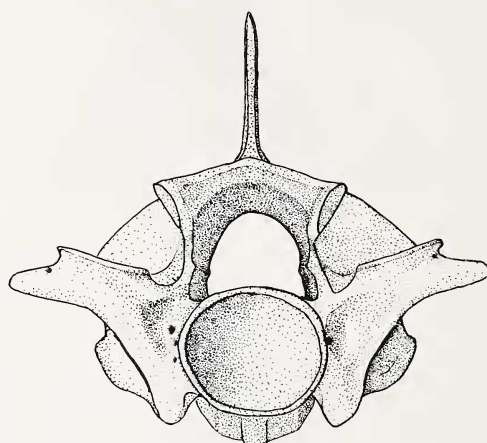
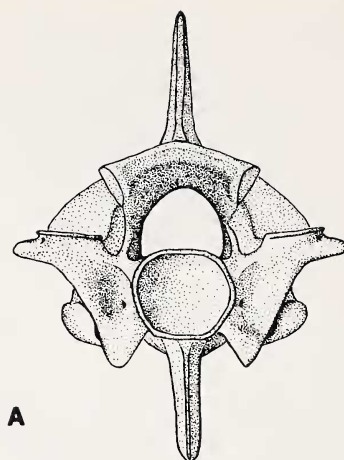


Figure 7. Comparison of anterior aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

Dissection has revealed (pers. obs.) that these fossae accommodate the segmental dilations of the longitudinal paravertebral internal lymphatic vessels described by Hoyer (Ottaviani and Tazzi, 1977). The segmentally dilated portions of these vessels

are connected by smaller diameter segments that pass between the parapophysis and the ventrolateral lip of the cotyle. This area is usually notched or grooved for reception of the narrowed segment (Fig. 5C, 7C, 13A, 13B). The notch is bounded

ventrally by a ligament that connects the ventral surface of the capitulum of the rib to the ventrolateral lip of the cotyle. A process may be developed on the ventrolateral cotylar lip for the attachment of this ligament in some individuals of certain species, but its presence is unpredictable. In some species, these notches and processes may be found in the posterior MTV series where the fossae are undeveloped. In its most anterior position, the notch is usually faint and of small diameter, but on progressively posterior vertebrae, it gradually increases in size and may even cause the emargination of the ventrolateral lip of the cotyle (Fig. 5C, 7C). The fossa is bounded laterally by the subcentral ridges and medially by the hemal keel (Fig. 5C, 13A). In most snakes the hemal keel is recessed slightly dorsal just posterior to the cotyle (Fig. 6C). This recess allows passage of the transverse anastomosing tracts of the longitudinal paravertebral internal lymphatic vessel. In species that possess PTV hypapophyses, the subcentral lymphatic fossae may be restricted to the anterior portion of the vertebra. Only one species examined in this study, *Lampropeltis getulus* (Linnaeus, 1766), has well developed fossae throughout the column (Fig. 12). Yet, even in this species, paracotylar notches are obviously enlarged in the PTV region.

The PTV tend to be somewhat more elongate than the MTV (Fig. 4B, 4C, 5B, 5C). Their zygopophyses are often produced laterally to a lesser extent. The neural canal and arch generally assume a broadened, more depressed form. The zygosphenes may become relatively broadened and crenate in shape, even in forms that have a flat zygosphenes in more cranial regions. In species that have high to medium height neural spines in the ATV and MTV, there is usually a significant decrease in height in the PTV that is particularly noticeable in the precloacal region. This decreased neural spine height is slight in species that have lower neural spines cranially. Hypapophyses, when present, are generally shorter and directed sharply caudad.

Precloacal Vertebrae (PCV). In many caenophidian species, there is a very small but distinctive region of three to five vertebrae, which immediately precedes the cloacal series. These vertebrae resemble the cloacal vertebrae in that they are abruptly foreshortened, but they lack the lymphapophyses diagnostic of cloacal vertebrae. PCV have low and short (craniocaudally) neural spines. Their neural arches tend to be more vaulted than those of the PTV. Finally, PCV have very pronounced notches between the parapophyses and cotyle, which usually emarginate the ventrolateral edges of the cotyle. Vertebrae of the cloacal region whose lymphapophyses are not fused greatly resemble PCV. They may be distinguished by their undivided, truncate paradiapophyses.

Cloacal and Postcloacal Vertebrae. The cloacal and postcloacal regions (Fig. 3), which are frequently lumped into the generalized category of “caudal vertebrae,” are not easily assigned to species or

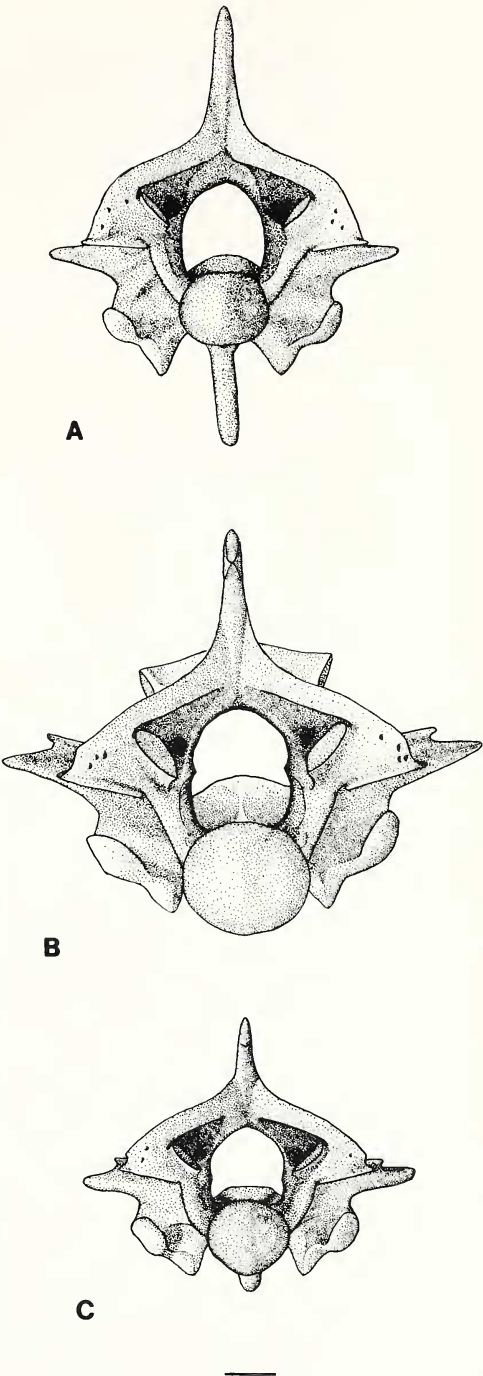


Figure 8. Comparison of posterior aspects of the three vertebrae illustrated in Figure 4. Bar = 1 mm.

genera. For this reason, they have not been considered in this study.

Ontogenetic Shape Change. Another category of morphological variability to be considered is ontogenetic shape change. The vertebrae of hatchling and very young snakes are distinctive from those

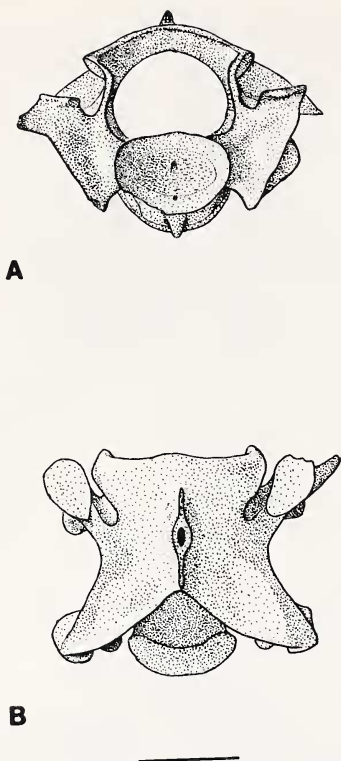


Figure 9. Fossil vertebra (LACMRLP 22109) of a very young juvenile *Pituophis melanoleucus* from Pit 91, Rancho La Brea. Bar = 1 mm.

of adult conspecifics and are easily distinguished from the vertebrae of adults of small species. Identification of hatchling specimens is not ordinarily a concern of the paleoherpetologist because their small, poorly ossified bones rarely fossilize. However, identification of these forms is a concern at Rancho La Brea where the conditions of preservation have allowed the recovery of the bones of several individuals that were very young (Fig. 9). Peculiarities of the vertebral morphology of hatchlings and young are described below in general terms.

Vertebrae of hatchling snakes may be distinguished by the thin, translucent nature of the bone (apparent even in the fossils). At hatching, vertebrae are little more than a thin shell of perichondral bone with some endochondral ossification (Winchester and d'A. Bellairs, 1977). In neonatal through subadult individuals, the endochondral ossification of the ends of the centrum (Winchester and d'A. Bellairs, 1977) can be distinguished as a circular area of lighter color in the center of the cotyle (pers. obs.).

Vertebrae of all recent hatchling snakes observed were relatively shorter than those of adults of the same species. This condition is most obvious in species such as *Coluber constrictor* Linnaeus, 1758, where vertebrae of adults are elongate, and less obvious in species that have relatively short verte-

brae as adults, e.g., *Arizona elegans* Kennicott, 1859 or *Elaphe obsoleta* (Say, 1823). Other features characteristic of hatchling snakes include a relatively enormous neural canal, a broad zygosphen, small zygapophyses that are not produced laterally, and a wide, shallow posterior notch in the neural arch (Fig. 9). Furthermore, some small or detailed features found in adults may not be apparent in hatchlings (i.e., epizygapophyseal spines). Regional differentiation of many characters is much less noticeable in hatchlings and may be almost obscured in some cases.

Vertebral shape change is rapid in young snakes and appears to decrease at about the same rate as growth. Vertebrae of young adults approach the characteristic shape of larger individuals but retain many vestiges of juvenile form, such as relatively shorter centra. Vertebral shape change appears to be continuous throughout life, although slow in mature individuals. Very large individuals of a species may appear hypermorphic (i.e., have very thickened bone, relatively small neural canals and foramina, exaggerated processes such as epizygapophyseal spines and accessory processes) when compared with smaller individuals.

SYSTEMATIC DESCRIPTIONS

Every attempt has been made to include as great a taxonomic and geographic diversity of comparative material as possible to identify potentially exotic or extinct forms. A list of comparative specimens used may be obtained from the author. Anatomical terminology of vertebrae is derived largely from Auffenberg (1963) and Hecht (1982); that of skull elements is from Cundall (1981) and Szyndlar (1984). Cranial muscle terminology follows Varkey (1979) (Fig. 10).

The systematic arrangement of subfamilies approximates that of Dowling and Duellman (1978). This arrangement was chosen because it provides a reasonable approximation of osteologically similar groups. Below the subfamily level, genera are divided into osteologically similar groups arranged in decreasing order of fossil abundance within groups. This arrangement is used to facilitate comparison and is not intended to reflect an opinion on phylogenetic relationships.

The species accounts provide descriptions of material that is definitively identifiable, including all skull elements, MTV, and PTV. Accounts are followed by descriptions of allocated material (i.e., ATV, PCV, and immature vertebrae), which is material that compares favorably with the assigned taxon but would not be definitively identified if considered in isolation.

Most vertebrae were assigned to the MTV subregion (the traditional standard of identification) unless they had distinct features of another subregion. Therefore, the MTV subregion is overrepresented in the materials listed below because of the inclusion of intermediate forms, and the ATV

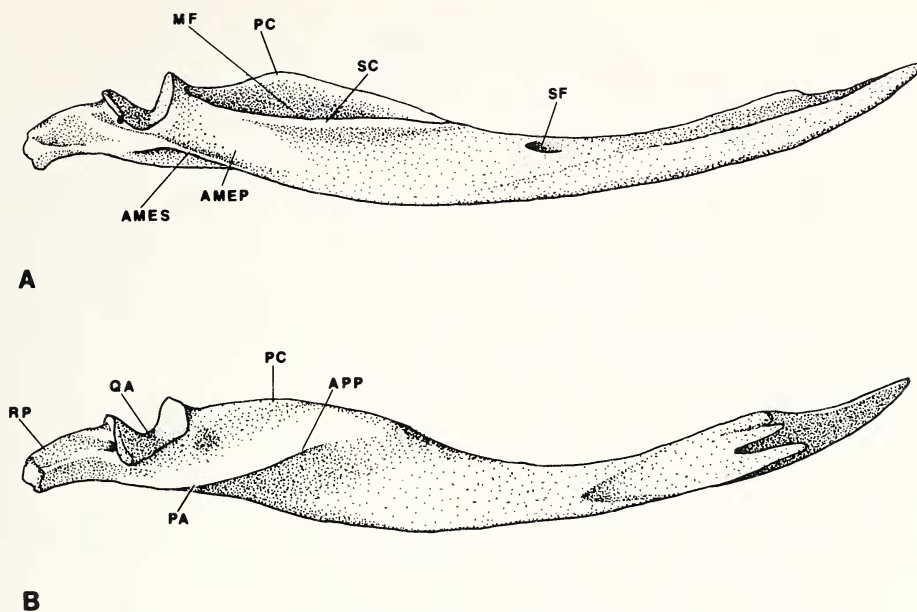


Figure 10. Right compound bone of *Nerodia sipedon sipedon*, illustrating terms used in text. **A.** Labial surface. **B.** Lingual surface. Abbreviations: AMEP = insertion of *M. adductor mandibulae externus profundus*, AMES = insertion of *M. adductor mandibulae externus superficialis*, APP = insertion of *M. adductor posterior: pars profundus*, MF = mandibular fossa, PA = insertion of *M. pterygoideus accessorius*, PC = prearticular crest, QA = quadrate articular facet, RP = retroarticular process, SC = surangular crest, SF = supraangular foramen. Bar = 1 mm.

and PTV subregions correspondingly are underrepresented. Vertebrae that were clearly immature are listed separately for each species with the subregion designation prefixed by the letter "I" (e.g., IMTV, etc.). Vertebrae representing specimens that are little differentiated from the condition in hatchlings were simply designated by "H" because regional differentiation is rudimentary at that stage. All fossil material is deposited at the Natural History Museum of Los Angeles County (LACMRLP).

Class REPTILIA Laurenti, 1768
 Subclass LEPIDOSAURIA Romer, 1945
 Order SQUAMATA Oppel, 1811
 Suborder SERPENTES
 Linnaeus, 1758
 Family COLUBRIDAE Cope, 1886
 Subfamily XENODONTINAE
 Cope, 1893
 Genus *Diadophis* Baird and Girard, 1853
Diadophis punctatus (Linnaeus, 1766)
 (Fig. 11, 12A)

REFERRED MATERIAL. Maxilla: 47445 (L); Compound bone: 52172 (R); MTV: 15694, 18293, 20278, 21562, 24307, 44507, 51928, 51961 (11), 52051, 52052, 52058, 52063 (5), 52071, 52076 (4), 52186 (2), 52192, 52195 (3), 52212 (10); PTV: 15554,

51578, 51961, 52051, 52063, 52076, 52195 (2), 52212 (4).

COMPARISONS. The maxilla of *Diadophis* (Fig. 11A) has a posterior diastema followed by two compressed, blade-like teeth that lack grooves or ducts. The shaft of the maxilla is bent laterally near the anterior end of the ectopterygoid process.

Sonora and *Chionactis* have shorter maxillary diastemata and weaker lateral bending. Other small colubrids examined lack a similar combination of diastema and lateral bending.

The shaft of the compound bone is bent slightly medially rostral to the mandibular fossa in *Diadophis* (Fig. 11B). The retroarticular process is directed medioventrally. The prearticular crest is highly arched, whereas the surangular crest is flat dorsally. The labial surface of the surangular crest is occupied by a distinct fossa that is bordered ventrally by a ridge. The fossa receives the insertion of the *M. adductor mandibulae externus profundus*. The ridge is continuous ventrally with the ventral surface of the compound and is the insertion of the *M. adductor mandibulae externus superficialis*. In large adults, a second ridge is located on the lingual surface running from near the ventral surface below the quadrate articulation, rostrally and dorsally, ending rostral to the prearticular crest. The anterior portion of this ridge is the insertion of the *M. adductor posterior: pars profundus*. The posterior portion of the ridge, which may be drawn into a tubercle (Fig. 11B) is the insertion of the *M.*

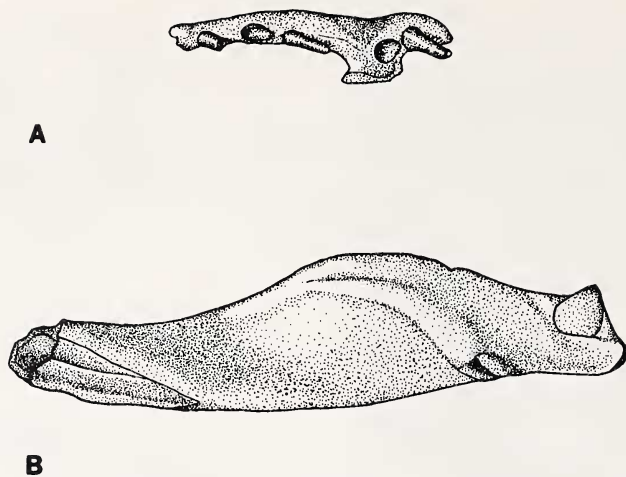


Figure 11. Fossil skull elements of *Diadophis punctatus* from Pit 91. A. LACMRLP 47445, left maxilla. B. LACMRLP 52172, right compound bone. Bar = 1 mm.

pterygoideus accessorius. The supraangular foramen (Szyndlar, 1984) is located a short distance rostral to the mandibular fossa.

Two other small North American snake species examined, *Hypsiglena torquata* (Gunther, 1860) and *Contia tenuis* (Baird and Girard, 1853), have the prearticular crest more highly arched than the supraangular crest. However, the prearticular crest is more highly arched in *Diadophis*. Also, *Contia* lacks the fossa of insertion for the *M. adductor mandibulae externus profundus*, whereas in *Hypsiglena* this fossa is reduced to a shallow horizontal groove. The ridge receiving the insertion of the *M. adductor posterior: pars profundus* and the *M. pterygoideus accessorius* was not observed in any specimens of *Hypsiglena* or *Contia*. Finally, the supraangular foramen is displaced rostrally in *Hypsiglena* and *Contia* relative to *Diadophis*.

The MTV of *Diadophis* (Fig. 12A) have been described by Auffenberg (1963). They are elongate

with depressed neural arches. The neural arch laminae are convex in posterior view. The neural arch notch is usually acute. The zygapophyses are moderately divergent. The accessory processes are short and blunt distally in large individuals. Auffenberg (1963) describes the hemal keel as oblanceolate or subspatulate. However, most comparative specimens observed had broader and flatter keels. The lateral edges of the hemal keel are often sloping and indistinct. *Diadophis* hemal keels may thus be better described as cunate or oblong *sensu* Auffenberg (1963:153). The neural spine is low and long but not obsolete posteriorly.

In *Diadophis* PTV, the centrum becomes relatively shorter than that of the MTV. Also, zygapophyses are less divergent, and the neural arch notch is more rounded in progressively posterior vertebrae. PTV cotyles and condyles are distinctly smaller than those of MTV. The sharpness of the edges of the hemal keel is accentuated by the sub-

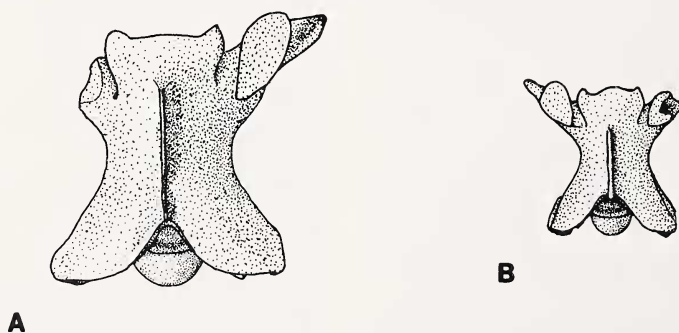


Figure 12. Comparison of dorsal aspects of fossil *Diadophis punctatus* LACMRLP 51961 (A) and *Tantilla* sp. LACMRLP 44374 (B) from Pit 91, Rancho La Brea. Bar = 1 mm.

central lymphatic fossae. The anterior region of the keel, just posterior to the ventral edge of the cotyle, is usually recessed dorsally to allow for the passage of the transverse anastomosing lymphatic duct. In some specimens, the neural spine becomes obsolete posteriorly in the PTV series.

Auffenberg (1963), Holman (1967, 1977b), Hill (1971), and Meylan (1982) discuss differences between the vertebrae of *Diadophis* and *Carphophis*, *Rhadinaea*, *Stilosoma*, and *Tantilla*. *Carphophis* MTV and PTV may generally be distinguished from those of *Diadophis* by their more depressed neural arches and lower neural spines that may be obsolete posteriorly, particularly in PTV. In *Rhadinaea* and *Stilosoma*, the accessory processes are directed approximately 90 degrees from the long axis of the centrum, whereas in *Diadophis* they are usually directed obliquely anteriorly. Meylan (1982:45) stated that the accessory processes of *D. punctatus* "... are hooked anteriorly and are not markedly pointed." However, examination of a broad geographic and ontogenetic series of individuals has shown these characters to be variable. Furthermore, several other genera have "hooked" accessory processes to some extent. Although there is some overlap, *Tantilla* (Fig. 12B) may often be distinguished from *Diadophis* by a lower neural spine that may be obsolete posteriorly (especially in the PTV), postzygapophyses that are distinctly longer than wide (only slightly longer than wide in *Diadophis*), and the obtuse posterior notch of its neural arch (acute notch in *Diadophis* MTV, Fig. 12A). The angle of this notch increases posteriorly in the PTV of both *Diadophis* and *Tantilla* such that they may still be distinguished by this character. Finally, the PTV of *Tantilla* are more elongate than those of *Diadophis*. The MTV and PTV of *Contia tenuis* may be distinguished from those of *Diadophis* by the relatively shorter centrum, the lower and thicker neural spines, and the more broadly rounded postzygapophyses of *C. tenuis*. Also, the distal tips of the laterally directed accessory processes tend to be more strongly hooked in *Contia* than in *Diadophis*.

The fossil material does not differ noticeably from modern *Diadophis punctatus*. It differs from the extinct *D. elinorae* Auffenberg, 1963 (material not seen) in its longer vertebrae with more depressed neural canals, weaker subcentral ridges, lower neural spines, and broader hemal keels. The neural spine of *D. elinorae* lacks an anterior overhang, a variable character in *D. punctatus*.

ALLOCATED MATERIAL. ATV: 52195; PCV: 52212; IMTV: 52063 (2), 52188; IATV: 52100, 52188.

COMPARISONS. The neural spine of ATV of *Diadophis punctatus* increases only slightly in height anteriorly. ATV hypapophyses are spine-like and directed caudally in the posterior region of the series. However, in the anterior region they become blade-like with a sinuous anterior edge.

Immature *Diadophis* vertebrae are generally less depressed and have hemal keels that are neither so

broad nor as flattened ventrally as those of adults. The accessory processes are relatively more elongate and acute in immatures.

DISCUSSION. This is the first record of *Diadophis punctatus* from the Pleistocene of California. *Diadophis punctatus* prefers relatively moist habitats, ranging from forest and woodland through chaparral and prairie, and inhabits arid habitat only along riparian corridors (Stebbins, 1985; Van Devender and Worthington, 1977). This species occurs in Los Angeles County today (Stebbins, 1985).

Genus *Tantilla*
Baird and Girard, 1853
***Tantilla* sp.**
(Fig. 12B)

REFERRED MATERIAL. MTV: 43748, 44374, 44617, 51965, 52059, 52210 (4); PTV: 52210 (2).

COMPARISONS. The vertebrae of *Tantilla* (Fig. 12B) are similar in shape to those of *Diadophis*. The MTV are usually elongate with convex neural arch laminae. The neural spines are low and may be obsolete posteriorly. The zygosphenes are usually strongly crenate. Accessory processes are generally thin and elongate. The hemal keel is broad, has sloping edges, and is often flattened ventrally.

Intracolumnar variability in *Tantilla* is essentially the same as noted for *Diadophis*, except the PTV tend to be more elongate in *Tantilla*.

In addition to the features mentioned under *Diadophis punctatus*, *Tantilla* may be distinguished by the smaller size of its vertebrae. Although there is size overlap between adult *Tantilla* and small *Diadophis* vertebrae, the latter usually have the distinctive features of young snakes, such as the enlarged neural canal, broader appearance, smaller zygapophyses, etc.

DISCUSSION. This genus is comprised of many widely scattered species that often have restricted ranges (Wilson, 1982). Many of these species are rather poorly known. No attempt was made to assign the fossil specimens to species because of the high degree of morphological similarity in this large genus and the lack of sufficient comparative material. The fossils do not differ noticeably from *Tantilla planiceps* (Blainville, 1834) known from southwestern California today.

This is the first record of *Tantilla* from the California Pleistocene. *Tantilla planiceps* is the only species found in the vicinity of Rancho La Brea today (Stebbins, 1985) and is found in woodland, grassland, chaparral, and desert habitats.

Genus *Hypsiglena* Cope, 1860
***Hypsiglena torquata* (Gunther, 1860)**

REFERRED MATERIAL. MTV: 14794, 20135, 35943, 39061, 51962 (4), 52064 (3), 52077 (2), 52088, 52211 (7); PTV: 52077, 50143.

COMPARISONS. *Hypsiglena torquata* vertebrae were described by Van Devender and Mead

(1978), Mead *et al.* (1984), and Van Devender *et al.* (1985). The MTV are relatively short and wide. The neural arch is depressed and has convex laminae. The neural canal is broad. Zygapophyses are produced laterally with unusually large, round facets. The neural spine is medium to low, with strong anterior and weaker posterior overhangs. The hemal keel is moderately narrow, strong, and rounded or flattened ventrally. Accessory processes are fairly elongate but blunt distally. They may be slightly hooked anteriorly.

Hypsiglena PTV have only moderate subcentral lymphatic fossae, yet the parapophyses are separated from the ventral edge of the cotyle by a pronounced notch. In the PTV, neural spines are lower and their cotyles and condyles are smaller than in the MTV.

Hypsiglena vertebrae are much shorter, their neural spines are less elongate and higher, and the hemal keel is less flattened and wider than in *Diadophis* or *Sonora*. *Hypsiglena* may be distinguished from *Phyllorhynchus* and *Rhinocheilus* by a more depressed neural arch. The zygapophyses of *Hypsiglena* are larger and are produced laterally more than those of *Sonora*, *Chionactis*, *Contia*, *Gyalopion*, *Chilomeniscus*, or *Ficimia*. The vertebrae of *Coniophanes fissidens* (Gunther, 1858) are similar to those of *H. torquata* but may usually be identified on the basis of the more pronounced interzygapophyseal ridge and lack of an anterior overhang on the neural spine.

ALLOCATED MATERIAL. ATV: 31214, 52081, 52152, 52194; PCV: 52093; IMTV: 52098; IPTV: 26260.

COMPARISONS. ATV postzygapophyses are even more laterally divergent than those of the MTV. The ATV neural arch laminae are convex, and their neural canal is large and rounded so that the ATV lack the overall depressed appearance of the MTV.

The zygosphenes of the PCV is very broad, its anterior edge arching strongly downward laterally, and its shape is strongly crenate. The zygapophyses are not produced laterally as strongly as in the MTV or PTV. The cotyles and condyles are very small.

In immature specimens, the hemal keel is gently rounded in transverse section. Large, rounded zygapophyses are evident even here.

DISCUSSION. Fossil material assigned to *Hypsiglena torquata* falls well within the range of variability noted above for the species. However, relative vertebral length was greater in some of the comparative material than in the fossils. Assignment to this species is based in part on geographic range because no other species of *Hypsiglena* were examined. The specific designation must therefore be regarded as tentative.

Pleistocene records of *H. torquata* from California include Redtail Peaks and Whipple Mountains (Van Devender and Mead, 1978). The habitat of this snake ranges from desert to woodland, including chaparral, creosote, sagebrush, grasslands,

and grass-sedge meadows (Wright and Wright, 1957; Stebbins, 1985; Conant, 1975). *Hypsiglena torquata* is found in the Los Angeles area today (Stebbins, 1985).

Subfamily COLUBRINAE Cope, 1895 Genus *Coluber* Linnaeus, 1758

Coluber constrictor Linnaeus, 1758

REFERRED MATERIAL. Maxilla: 41901 (L); Compound bone: 14208 (R); MTV: 10066, 14304, 16976, 19474, 22040, 22241, 22565, 29148, 37999, 39737, 41241, 47324, 51941, 51966, 52070, 52074, 52082 (6), 52108 (2), 52111 (2), 52116, 52162, 52180 (2), 52216 (8); PTV: 51917, 51941, 52082, 52092, 52111 (4), 52216 (6).

COMPARISONS. *Coluber* has 13–17 maxillary alveoli ($n = 36$ maxillae, 20 individuals) and lacks a diastema.

The maxilla of *Coluber* may be distinguished from that of *Masticophis* by its shorter palatine process that spans roughly two alveoli. *Masticophis* has 16–20 maxillary alveoli ($n = 30$, 16 individuals, five species) and a palatine process that generally spans two and one-half to three alveoli. Differentiation from *Pituophis* and *Arizona* is described under *Pituophis*. *Rhinocheilus*, *Diadophis*, and *Salvadora* all possess diastemata.

The compound bone of *Coluber* has prearticular and surangular crests of roughly equal height. The ventral surface of the bone is rounded in the vicinity of the quadrate articulation.

Masticophis, *Rhinocheilus*, and some *Lampropeltis getulus* also have prearticular and surangular crests of approximately equal height. In *Rhinocheilus*, the crests are lower than in *Coluber*. The ventral border of the compound bone of *Masticophis* narrows to a keel below the quadrate articulation but is wider and rounded in *Coluber*. *Lampropeltis getulus* has a narrower mandibular fossa than does *Coluber*.

The vertebrae of *Coluber* have been discussed by Holman (1962), Auffenberg (1963), and Meylan (1982). I have found that the MTV of *C. constrictor* are geographically variable; however, some features are shared by all specimens examined. The MTV are elongate, with a moderately vaulted neural arch. Neural arch laminae range from strongly convex to nearly flat. The neural canal may be rectangular in outline or narrowed dorsally. Epizygapophyseal spines are moderately developed to very strong. The neural spine is elongate, medium to low in height, and often has moderate anterior and posterior overhangs. Accessory processes are long, thin to thick, and acute or blunt distally. Subcentral ridges are usually strong. The hemal keel is well developed and spatulate. Vertebrae of smaller forms are usually more elongate and gracile, with smaller epizygapophyseal spines.

The PTV of *Coluber* are more depressed than the MTV. The accessory processes remain long and

are usually thick and blunt distally. Subcentral lymphatic fossae may be very strongly developed or only moderately developed and restricted to the anterior half of the centrum. Subcentral ridges may vary from strong (in forms with strong subcentral lymphatic fossae) to weak and restricted to the anterior region of the centrum. The hemal keel is thick, it may be produced from the centrum, and its cross-sectional outline is squared.

Coluber and *Masticophis* have very similar vertebrae, but as a group they may be separated from most other North American colubrid genera by their relatively greater vertebral length. *Ophedrys* and *Salvadora* also have relatively elongate vertebrae, but *Ophedrys* lacks epizygapophyseal spines (Holman, 1962), whereas *Salvadora* has slightly shorter vertebral centra and relatively smaller condyles (Holman, 1970, 1976). *Drymarchon corais* (Boie, 1827) and *Spilotes pullatus* (Linnaeus, 1758) are readily differentiated from *Coluber* and *Masticophis* by their more robust appearance. Neither the *Drymarchon* nor *Spilotes* examined were as elongate as *Coluber* and *Masticophis*. Furthermore, the neural spine of *D. corais* is usually beveled anterodorsally (Auffenberg, 1963; Meylan, 1982), whereas *S. pullatus* lacks epizygapophyseal spines. *Drymobius margaritiferus* (Schlegel, 1837) is quite similar to racers in its vertebral morphology. However, *D. margaritiferus* consistently has a larger, rounded neural canal and a zygosphenoid that is correspondingly broader. The zygapophyses have smaller facets and are not produced laterally in *Drymobius* as extensively as in *Coluber* and *Masticophis*.

Several authors (see Holman, 1981:266) have indicated that the similarity between *Coluber* and *Masticophis* is too great to reliably distinguish between them. However, examination of a large series of specimens of broad geographic scope has indicated that there are enough consistent differences, at least on a regional basis, to allow reliable differentiation. *Coluber constrictor mormon* Baird and Girard, 1852 of the western United States appears to be particularly distinctive. It is a relatively small subspecies, but its vertebrae are not as elongate as those of other small racers. Furthermore, its zygapophyses are not produced as far laterally as in most *Masticophis* species. Its epizygapophyseal spines are small, and the neural arch is somewhat depressed. The subcentral ridges are strong and convex laterally in ventral view, giving the centrum a flattened ventral surface. The postzygapophyses are generally elevated above the level of the dorsal edge of the condyle. Finally, the accessory processes are directed nearly laterally.

The smaller, more gracile forms of *Masticophis* [e.g., *M. taeniatus* (Hallowell, 1852) and *M. lateralis* (Hallowell, 1853)] are similar to *C. constrictor mormon* but differ as follows: vertebrae more elongate, zygapophyses produced laterally to a greater degree, neural arch more vaulted, subcentral ridges not as strongly developed and smoothly converging

posteriorly, postzygapophyses not (or barely) elevated above condyle, accessory processes directed anterolaterally.

Larger racers (e.g., *C. c. constrictor*, *C. c. foxi* Baird and Girard, 1853, *C. c. priapus* Dunn and Wood, 1939, and *M. flagellum* ssp.) are readily distinguished from smaller racers. They have more robust vertebrae with highly vaulted neural arches, zygapophyses produced farther laterally than in the smaller racers, and higher neural spines.

Obviously, the vertebral morphology of racers needs a great deal more attention. Although the discriminant analysis of Meylan (1982) was partly successful, I believe that a more detailed morphometric analysis among recognized taxa will provide improved results.

ALLOCATED MATERIAL. ATV: 51953, 52085, 52096, 52145.

COMPARISONS. The anterior ATV of *Coluber* are shorter than the MTV, yet more elongate than ATV of many other genera (e.g., *Arizona*, *Pituophis*, *Elaphe*, etc.). The prezygapophyses are small and ovoid, with their long axes craniocaudally directed. Postzygapophyses are small and rounded. Accessory processes are very short, acute, and craniolaterally directed. Neural spines are of moderate length and may have posterior overhangs. The hypapophyses are long, ventrally directed, and squared distally. In the posterior ATV series, most characters are intermediate between anterior ATV and MTV. Here the hypapophysis becomes more posteriorly directed, its anteroventral surface approximates the sinuous condition, and its distal tip becomes obtusely pointed. *Coluber* ATV were distinguished from those of *Masticophis* largely on the basis of their shorter length and laterally convex subcentral ridges.

Because of much greater interspecific similarity and a general lack of comparative material, the vertebrae of immature racers were assigned to the category "*Coluber* or *Masticophis*," below.

DISCUSSION. Fitch *et al.* (1981) have suggested that *Coluber constrictor mormon* should be restored to full species status on the basis of differences in its morphology and various reproductive parameters from other *C. constrictor* subspecies. Yet, other authors (Greene, 1984; Corn and Bury, 1986) have provided evidence of intergradation between *C. constrictor flaviventris* and *C. constrictor mormon* in certain areas in the Rocky Mountains region. The species is here interpreted in the broad sense for convenience. Because the fossil vertebrae represent a population quite similar to modern *C. c. mormon*, which inhabits the Los Angeles region today, and are less similar to observed morphological variants of other *Coluber* or *Masticophis*, it is reasonable to assign these fossils to the more inclusive taxon, *C. constrictor*.

Brattstrom (1953b:376) identified "one partly damaged lower jaw . . ." from Rancho La Brea as "*Coluber* sp. (*sensu lato*)."

Here he implies the inclusion of *Masticophis* within *Coluber*. Vertebrae

from Rancho La Brea were later assigned to *Coluber constrictor* by Brattstrom (1958). The only other record of *Coluber* from the California Pleistocene is a single vertebra from the Carpinteria asphalt deposits (Brattstrom, 1955). Stebbins (1985) indicates that western forms of this species prefer semiarid to moist open habitats such as meadows, prairies, and thin brush, but they avoid xeric habitats.

Genus *Masticophis*
Baird and Girard, 1853
Masticophis lateralis
(Hallowell, 1853)

REFERRED MATERIAL. MTV: 12166, 15887, 16126, 21016, 48181, 52178, 52217; PTV: 25869, 52184 (2).

COMPARISONS. The MTV of *Masticophis* are discussed by Auffenberg (1963), Hill (1971), Meylan (1982), and Mead *et al.* (1984). MTV are elongate. Neural arches are moderately vaulted to moderately depressed. Neural arch laminae are flat or convex. The neural canal is generally large and subquadratic in outline from anterior, with the dorsal border only slightly narrower than the ventral. Zygapophyses tend to be relatively small, rounded, and divergent. The neural spine is long and varies from moderately high to low. Accessory processes are elongate, thick to moderately thick, and blunt distally. Subcentral ridges are moderate to strong. The centrum is smoothly tapered posteriorly. The hemal keel is low or produced ventrally, thin, and generally spatulate.

Intracolumnar variability is similar to that described for *Coluber constrictor*. Immature racer vertebrae were assigned to the “*Coluber* or *Masticophis*” category. Identification of *Coluber* and *Masticophis* to the generic level is discussed under *Coluber*.

Masticophis lateralis may often be distinguished from *M. taeniatus* by its narrower neural canal, slightly smaller epizygapophyseal spines, and thicker neural arch laminae.

DISCUSSION. Jennings (1983) mentions this first known fossil record of *Masticophis lateralis*. Stebbins (1985) describes this species as an inhabitant of the foothills and, occasionally, forested regions and mountains. It prefers chaparral associations but also frequents grassy, brushy, or rocky areas, especially areas near freshwater (Wright and Wright, 1957; Stebbins, 1985). *Masticophis lateralis* occurs in Los Angeles County today (Stebbins, 1985).

Coluber sp. or *Masticophis* sp.

REFERRED MATERIAL. ATV: 20893, 52145, 52198 (2), 52203, 52219; MTV: 11439 (fragment), 15508, 15992, 17701, 17768, 33437 (fragment), 41386, 51948, 51954 (3), 51966 (3), 52198, 52219 (6); PTV: 25007 (fragment), 48935, 51948 (2), 52060 (2), 52187; IMTV: 24608, 30800, 48094, 51966 (2),

52103, 52181 (2), 52190, 52198, 52203 (2), 52219 (3); IPTV: 52065, 52206, 52219 (2); H: 39745, 52136, 52219.

COMPARISONS. These vertebrae represent *Coluber* or *Masticophis* but are either too fragmentary to assign to species or fall within the range of overlap of both.

Vertebrae of immature racers were all assigned to this category because of a lack of immature comparative material. Vertebrae of immature racers are not quite as short as those of most other immature colubrids. Accessory processes are moderately long and pointed distally. Cotyles and condyles are relatively small. Hatchling racers have vertebrae that are nearly as short as those of any other colubrid species, but they may usually be distinguished by their broad and shallow posterior neural arch notch, small and divergent postzygapophyses, and a broad centrum with subcentral ridges apparent but subcentral lymphatic fossae lacking. The hemal keel in hatchling racers is generally broad and indistinct.

Genus *Pituophis* Holbrook, 1842
Pituophis melanoleucus
(Daudin, 1803)

(Fig. 9)

REFERRED MATERIAL. Maxilla: 42641 (L), 51945 (IL), 51958 (IL); Pterygoid: 51922 (fragmentary R); Compound bone: 24461 (R); MTV: 14266, 14923, 15419, 16307, 17607, 18047, 18786, 18865, 19178, 20048, 21208, 21401, 22018, 23008, 23160, 23652, 23935, 24471, 24645, 25957, 25978, 26982 (fragment), 27718, 30214, 30447, 32393, 37225, 38570, 39618, 42025, 47713, 48877, 51926, 51934, 51950, 51964, 52123 (4), 52164 (fragment), 52215 (8); PTV: 14971, 16405, 16584, 16852, 17704, 18907, 20048, 21436, 21825, 23505, 23848, 30930, 33306, 34743, 37716, 42621, 50543, 51921, 51927, 51940 (2), 52123, 52215 (8).

COMPARISONS. The maxilla of *Pituophis* has 17 (rarely 16) alveoli, a posteriorly placed palatine process, and a long ectopterygoid process. The only other genera examined with similar alveolar counts are *Masticophis* and *Coluber* with 17–19 and 14–16 alveoli, respectively. *Pituophis* may be separated from these by the length of its ectopterygoid process, which spans four alveoli. In *Masticophis* and *Coluber*, it spans only two or two and one-half. The maxilla of *Pituophis* is also distinctive in that the palatine process occurs at a point about two-fifths down the length of the bone. This character is shared with *Arizona*, but here the process lies opposite the sixth alveolus, whereas in *Pituophis* it lies opposite the eighth or part of the seventh and eighth alveoli. The *Arizona* maxillae examined had lower alveolar counts (14) than *Pituophis*.

In *Pituophis*, the pterygoid tooth row extends less than half the length of the bone. *Arizona* is the only other genus observed that shares this fea-

ture with *Pituophis*. The two differ in that the dorsal crest is much better developed in *Arizona*.

In *Pituophis*, the prearticular crest of the compound bone is more elevated than the surangular crest but is only moderately arched. The crests are about equal in *Coluber*, *Masticophis*, *Rhinocheilus*, and some specimens of *Lampropeltis getulus*. *Thamnophis*, *Salvadora*, and *Arizona* have an elevated prearticular crest as in *Pituophis*, but it is more arched. In some specimens of *Lampropeltis getulus*, the prearticular crest is elevated, but the dorsal opening of the mandibular fossa is always narrower than in other large colubrids.

The MTV of *Pituophis* are moderately short to moderately elongate. The neural arch is moderately vaulted, and its laminae are convex. The neural canal is higher than wide from anterior view and usually wider ventrally than dorsally. Zygapophyses are moderately divergent. The zygosphenes are usually convex dorsally. Neural spines are of medium height in the western subspecies examined but higher in eastern subspecies (especially *P. m. mugitus* Barbour, 1921). Accessory processes are short and acute. Epizygapophyseal spines are obsolete to absent. The hemal keel is low, narrow, and spatulate to gladiate. Subcentral ridges are weak to moderate.

PTV are noticeably more elongate than MTV. The neural arch retains approximately the same degree of vaulting as in MTV but has less convex laminae. The hemal keel is produced ventrally and may become gladiate.

Criteria for identification of *Pituophis* vertebrae have been discussed by Auffenberg (1963), Holman (1965), Van Devender and Mead (1978), Meylan (1982), and Mead *et al.* (1984). Among western colubrids, *Pituophis* vertebrae are most readily confused with *Arizona*, *Elaphe*, or *Lampropeltis getulus*. The MTV of *L. getulus* have distinct lymphatic fossae ventrally. This character is only present in the PTV of *Pituophis*. The PTV of *Pituophis* are readily distinguished from those of *L. getulus* by their vaulted neural arches and thin accessory processes. Weaker subcentral ridges will distinguish *Pituophis* from most species of *Elaphe*. *Pituophis* vertebrae are generally more elongate than those of *Arizona*. However, this character varies with age such that very young specimens overlap strongly with mature *Arizona*. Finally, immature *Pituophis* condyles are much larger than those of similar sized *Lampropeltis*, *Elaphe*, or *Arizona*. This character appears to change ontogenetically, large specimens not sharing the exaggerated condyle.

ALLOCATED MATERIAL. ATV: 15041, 18490, 50295, 51636, 51929, 52189 (2), 52208, 52215 (4); IATV: 52140, 52189 (2), 52202, 52204; IMTV: 10504, 15419 (6), 20301, 51919, 51921, 51923 (3), 51931 (7), 51933, 51934, 51939, 51964, 52122, 52179 (4), 52196 (2), 52202, 52208, 52215 (6); IPTV: 23847, 25652, 51956, 52087, 52189; H: 15419, 16475, 22109, 35979, 52087.

COMPARISONS. Anterior ATV have a highly vaulted neural arch. Accessory processes are short

and acutely pointed. Cotyles and condyles are small. The hypapophysis is long, ventrally directed, and squared distally. The hypapophysis regresses in length posteriorly in the ATV series but remains ventrally directed and squared distally.

Vertebrae of hatchlings (Fig. 9) are extremely short. The neural arch is moderately vaulted with laminae that are slightly convex laterally. The neural canal is higher than wide and wider ventrally than dorsally. Postzygapophyses are elevated above the condyle, and prezygapophyseal buttresses are very high. The zygosphenes are convex dorsally. Accessory processes are long, thin, and sharply pointed. Condyles and cotyles are relatively larger in this species than in any other observed at this stage of development.

DISCUSSION. Brattstrom (1953b) reported *Pituophis melanoleucus* (as *P. catenifer*) from Rancho La Brea. Other late Pleistocene localities in California include the McKittrick Asphalt (Brattstrom, 1953a) and Costeau Pit (Hudson and Brattstrom, 1977).

Pituophis melanoleucus is known from most habitat types and to relatively high elevations throughout its wide range. It is found in Los Angeles County today (Stebbins, 1985).

Genus *Arizona* Kennicott, 1859

Arizona elegans Kennicott, 1859

REFERRED MATERIAL. MTV: 51932, 52163, 52214; PTV: 52214.

COMPARISONS. MTV of *Arizona* have been described by Van Devender and Mead (1978) and Mead *et al.* (1984). They are short and broad with a moderately vaulted neural arch and a wide neural canal. Neural arch laminae are distinctly convex laterally. The neural spine is medium in height. Accessory processes are of medium length and relatively thin. The condyle is moderately wide and the subcentral ridges are moderately developed. The hemal keel is distinct, low, and spatulate.

PTV of *Arizona* are not distinctly more elongate and do not have noticeably lower neural spines than MTV. The notch between parapophyses and ventrolateral cotyle is minimally developed except near the PCV series. However, subcentral lymphatic fossae are well developed on the anterior portion of the centrum, and the hemal keel is deep and narrow.

Arizona vertebrae most closely resemble those of *Pituophis*. The criteria used to distinguish these two genera are discussed under *Pituophis*. Holman (1963) discussed the distinction between *Arizona elegans* and several species of *Lampropeltis*. *Arizona* vertebrae differ from those of *Elaphe* in that they are shorter and have weaker subcentral ridges in the MTV series. Also, the neural arch laminae are convex laterally in *Arizona*, whereas they are simply convex in *Elaphe*.

ALLOCATED MATERIAL. H: 46221.

COMPARISONS. Immature *Arizona* vertebrae are only slightly shorter than those of adults. Their

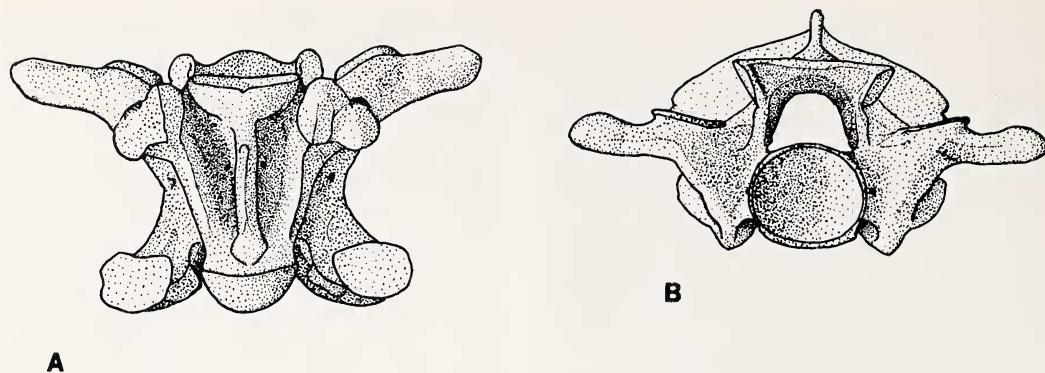


Figure 13. Fossil vertebra (LACMRLP 51960) of *Lampropeltis getulus* from Pit 91, Rancho La Brea. A. Ventral aspect. B. Anterior aspect. Bar = 1 mm.

condyles and cotyles are of moderate size. The enlarged neural canal is slightly higher than wide.

DISCUSSION. This species has not previously been reported from the Pleistocene of California.

Arizona elegans prefers open areas with chaparral, sagebrush, or grassy vegetation or barren deserts. Its present range includes Los Angeles County (Stebbins, 1985).

Genus *Lampropeltis* Fitzinger, 1843 *Lampropeltis getulus* (Linnaeus, 1766)

(Fig. 13)

REFERRED MATERIAL. Maxilla: 51925 (IL fragment); MTV: 14948, 19994, 20151, 28575, 51938, 51960, 52069 (2), 52080 [3 (2 fused)], 52114 (2); PTV: 40284 (3), 51938, 52107, 52126.

COMPARISONS. Maxillae of *Lampropeltis* are short, robust, generally contain 13–15 alveoli ($n = 9$), and lack diastemata. The palatine process is long, narrow, directed posteriorly, and located about one-third the maxillary length back from the anterior end. Anteriorly, the maxilla is high and narrow.

Pituophis and *Arizona* have longer, thinner maxillae, with palatine processes located more posteriorly. *Pituophis* usually has 17 maxillary alveoli. *Masticophis* and *Coluber* also have longer maxillae, with wider palatine processes that are directed medially. *Masticophis* has 17–19 maxillary alveoli. The anterior portion of the maxilla in *Rhinocheilus*, *Lampropeltis triangulum* (Lacepede, 1788), *L. pyromelana* (Cope, 1866), and *L. zonata* (Lockington, 1876) is more depressed than in *L. getulus*.

Lampropeltis getulus vertebrae (Fig. 13) have been discussed by Auffenberg (1963), Holman (1965), Van Devender and Mead (1978), Meylan (1982), and Mead *et al.* (1984). Their MTV are moderately short and broad. The neural arch is moderately depressed, with laminae that are flat to slightly convex laterally. The zygapophyses are moderately to strongly produced laterally. The neural spine is of medium height and generally has an angular over-

hang posteriorly. In large specimens, the neural spine may be thickened dorsally. Cotyles and condyles are of moderate size. Accessory processes are long, very thick, and blunt distally. This species is peculiar in that the dorsoventral diameter of the accessory processes may abruptly increase distally in mature specimens (Fig. 13B). The hemal keel is usually strongly produced ventrally, thin, and spatulate to gladiate. Subcentral ridges are strongly developed and are accentuated by the deep subcentral lymphatic fossae that are present throughout the column. Notches are often present between the cotyle and parapophyses throughout the MTV and PTV. In large specimens, lateral processes from the ventrolateral lip of the cotyle may nearly contact the ventral edge of the parapophysis, causing the notch to approximate a foramen.

PTV of *Lampropeltis* are not nearly so well differentiated from MTV as in most species. They are more elongate, with more depressed neural arches. Subcentral lymphatic fossae are somewhat deeper, and paracotylar notches are large and well developed, causing emargination of the ventrolateral lip of the cotyle.

Vertebrae of *Lampropeltis getulus* may be distinguished from those of *Pituophis* as described above. *Arizona* and *Elaphe* are readily distinguished from *Lampropeltis getulus* by their shorter vertebrae that lack subcentral lymphatic fossae on the MTV. In *Lampropeltis* PTV, the centra are slightly more elongate, the neural arches more depressed, the zygapophyses more divergent, and the accessory processes longer and larger in diameter than in either *Elaphe* or *Arizona*. Vertebrae of *Rhinocheilus lecontei* are similar to those of *Lampropeltis getulus* but are distinguished by being shorter and having wider hemal keels, weaker subcentral lymphatic fossae, smaller zygapophyses, and shorter neural spines.

Vertebrae of other *Lampropeltis* species have weaker hemal keels and subcentral lymphatic fossae. They also lack thickened neural spines and

accessory processes. Furthermore, vertebrae of *L. triangulum* and related forms are more elongate and depressed.

ALLOCATED MATERIAL. IATV: 52185; IMTV: 27777, 52057, 52080, 52185, 52200.

COMPARISONS. Anterior ATV of *Lampropeltis getulus* have moderately depressed neural arches that have laterally convex laminae. The posterior neural arch notch is shallow and obtuse. Zygapophyses are not divergent. Accessory processes are short, thick, and blunt. Cotyles and condyles are very small. Hypapophyses are long, ventrally directed, and squared distally. Subcentral lymphatic fossae are present, but shallow; anterior lymphatic notches are negligible.

In immature vertebrae, the neural canal is high and the cotyle is slightly depressed. The zygosphenoid is convex dorsally. The hemal keel is relatively broad, low, and rounded in transverse outline, its lateral borders sloping and indistinct. Subcentral ridges are moderately distinct. Subcentral lymphatic fossae are present anteriorly in the region of the subcentral foramen but are not as distinct as in adults. Anterior lymphatic notches are poorly developed.

DISCUSSION. Brattstrom (1953b, 1958) reported *Lampropeltis getulus* from Rancho La Brea. Other reports from California include McKittrick (Brattstrom, 1953a), Newport Beach Mesa (Hudson and Brattstrom, 1977), and Redtail Peaks and Tunnel Ridge (Van Devender and Mead, 1978).

Lampropeltis getulus is a very wide ranging species throughout the southern half of the United States. It occupies most terrestrial habitats within its range (Wright and Wright, 1957). It is found in Los Angeles County today (Stebbins, 1985).

Genus *Rhinocheilus*
Baird and Girard, 1853
Rhinocheilus lecontei
Baird and Girard, 1853

REFERRED MATERIAL. MTV: 52115 (3).

COMPARISONS. Vertebrae of this monotypic genus have been described by Hill (1971), Van Devender and Mead (1978), and Mead *et al.* (1984). *Rhinocheilus* vertebrae are short to moderately elongate. Their neural arches are moderately depressed, but have strongly convex laminae. Zygapophyses are rather small and only moderately produced laterally. The zygosphenoid is flat dorsally, and crenate anteriorly. The neural spine is of medium height, thickened dorsally, and has strong anterior and posterior overhangs. Accessory processes are long, thick, and blunt and may be thicker distally than proximally as in *Lampropeltis getulus*. The hemal keel is strong and spatulate and has well defined lateral edges. Subcentral lymphatic fossae are present throughout the column but are not as strong as in *L. getulus*.

PTV of *Rhinocheilus* are of approximately the same relative length as MTV. Zygapophyses are less divergent in the PTV, and the cotyle and condyle

are smaller. However, accessory processes are relatively larger. The hemal keel is produced ventrally.

This species most closely resembles *Lampropeltis getulus*, but may be distinguished from it as described under that account. *Hypsiglena* vertebrae are smaller and more depressed and have relatively larger and more laterally produced zygapophyses.

ALLOCATED MATERIAL. ATV: 52191.

COMPARISONS. ATV of *Rhinocheilus* have slightly more vaulted neural arches than MTV with extremely convex laminae. The posterior neural arch notch is moderately deep and slightly obtuse. The zygosphenoid is crenate but may be slightly convex dorsally. Zygapophyses are small and not divergent. The neural spine is slightly higher than in MTV, its anterior border is vertical, and its posterior border retains a strong overhang. Accessory processes are short, laterally directed, and blunt. The hypapophysis is long, ventrally directed, and rounded distally.

DISCUSSION. *Rhinocheilus lecontei* was reported from Tunnel Ridge in California (Van Devender and Mead, 1978). Stebbins (1985) lists deserts, prairies, and brushland as habitats for this nocturnal species. It is known from the Los Angeles area today (Stebbins, 1985).

Subfamily NATRICINAE
Bonaparte, 1840
Genus *Thamnophis* Fitzinger, 1843
Thamnophis couchii species complex
(after Rossman and Stewart, 1987)

REFERRED MATERIAL. MTV: 15038, 15974, 16046, 17242, 46925, 51944 (3), 51952 (3), 52072, 52083, 52101 (13), 52106, 52129, 52131, 52133; PTV: 18859, 23075, 23133, 30100, 51944, 52095, 52101, 52166.

COMPARISONS. The MTV of members of the *Thamnophis couchii* complex are moderately elongate to short. The neural arch is moderately vaulted, and its laminae are slightly convex. Zygapophyses are produced laterally. Epizygapophyseal spines are moderately developed to absent. Neural spines are medium in height but short, with moderate anterior and strong to moderate posterior overhangs. Accessory processes are typically medium in length and acute distally. Hypapophyses are short, blade-like, and obtusely pointed posteroventrally, and the anteroventral edge is often strongly angular. Subcentral ridges are moderate to strong. The lymphatic notch is often present throughout the column. Ventrolateral processes are often present on the lip of the cotyle.

Great variability and a large degree of overlap in features makes specific identification of *Thamnophis* vertebrae difficult. Holman (1962) used characters of the neural spine to identify certain species groups within the genus. Members of the *Thamnophis couchii* group and *Thamnophis sirtalis* (Linnaeus, 1758), which live in the Los Angeles area

today, have neural spines that are somewhat longer than high and usually lack strong anterior overhangs, although the anterior border may be slightly inclined forward. Anterior overhangs are strongly developed in the western species *T. elegans* (Baird and Girard, 1853), *T. eques* (Reuss, 1843), and *T. marcianus* (Baird and Girard, 1853). *Thamnophis cyrtopsis* (Kennicott, 1861) has a much lower, longer neural spine.

The members of the *Thamnophis couchii* group display a wider range of vertebral morphology than any other species group of *Thamnophis* examined. Most of the referred specimens have the weak or absent anterior overhangs of the *T. couchii* group and *T. sirtalis*.

Most of the specimens of the *T. couchii* group available for comparison were relatively large individuals (e.g., *T. gigas* Fitch, 1940). These were easily distinguished from *T. sirtalis* on the basis of the shorter centra and more laterally produced zygapophyses of the former. However, the smallest individuals tend to converge in shape because the elongate character of the centrum of *T. sirtalis* is less distinct in young individuals, becoming more pronounced with age. Much of the fossil material represents snakes that are smaller to much smaller than most of the comparative specimens of the *T. couchii* group available and falls within the range of shape overlap. The bulk of the fossil material appears to represent a single population of relatively small individuals that are, on the whole, closer to the *T. couchii* group than to *T. sirtalis*. Yet, some specimens were much larger than the rest and clearly represent *T. sirtalis*. A conservative approach was adopted in assigning these specimens. Most fell near the range of shape overlap and were assigned only to genus (*Thamnophis* sp., below). Others matched the extreme condition seen in the *T. couchii* group and were clearly unlike any *T. sirtalis* specimens observed. These were assigned to the *T. couchii* group. Intracolumnar and ontogenetic variation are approximately as described under *Thamnophis* sp.

DISCUSSION. Until recently, the members of the *T. couchii* group were considered to be subspecies of a single variable species, *T. couchii* (Fitch, 1984). Rossman and Stewart (1987), on the basis of detailed morphological studies and the biochemical evidence of Lawson and Dessauer (1979), have accorded four of these subspecies full species status: *T. couchii*, *T. hammondii* (Kennicott, 1860), *T. gigas* Fitch, 1940, and *T. atratus* (Kennicott, 1860) (with three subspecies). Although members of this group share certain vertebral characters, a more detailed morphometric analysis of larger samples will be required to determine whether these species can be reliably separated from each other on the basis of isolated vertebrae. Clearly, a form allied to the semiaquatic *T. couchii* had differentiated from the more terrestrial *T. elegans* and *T. sirtalis* groups by the time period of the Pit 91 deposit.

No member of the *Thamnophis couchii* group

has previously been reported from the fossil record. Most species of the *T. couchii* group are semiaquatic, living near marshes and streams and feeding principally on fish and anuran larvae (Fitch, 1984). In this regard, their ecology resembles that of many members of the genus *Nerodia*. *Thamnophis hammondii* is found in the Los Angeles area today (Stebbins, 1954, 1985).

Thamnophis sirtalis (Linnaeus, 1758)

REFERRED MATERIAL. MTV: 18048, 20485, 51943, 52128, 52174 (3).

COMPARISONS. *Thamnophis sirtalis* MTV are moderately to very elongate. The neural arch is vaulted and its laminae are convex. Zygapophyses are moderately produced laterally. Epizygapophyseal spines are typically well developed. The neural spine is of medium height with strong posterior overhangs and weaker anterior overhangs. Accessory processes are medium to long, thick, and blunt. Hypapophyses are short, blade-like, and directed strongly caudad. The anteroventral surface is strongly sinuous. Subcentral ridges are very prominent. Notches between the parapophyses and the ventrolateral lip of the cotyle are well developed throughout the column. Small processes often project from the ventrolateral lip of the cotyle.

DISCUSSION. The fossil material is indistinguishable from the comparative material examined. *Thamnophis sirtalis* has not previously been reported from the Pleistocene of the Southwest. This widespread species is usually found near aquatic or mesic environments, ranging into fields and woodlands. Dixon (1967) reported only two records of this species historically in Los Angeles County, which is near the southernmost extent of its present range in California (Stebbins, 1985).

Thamnophis sp.

REFERRED MATERIAL. Maxillae: 41286 (L, fragment), 52169 (L, fragment), 47727 (R), 51936 (R), 51959 (R); palatine: 41212 (L); pterygoid: 17455 (R, pathologic); dentaries: 51947 (R, distal fragment), 52171 (R); compound bone: 52084 (R); MTV: 10074, 12542, 12783, 13475, 13799, 14154, 14629, 14980, 14997, 15233, 15453, 15475, 15600, 15662, 15680, 15760, 15771, 15807 (fragment), 15810, 15872, 15946, 15984, 16002, 16058, 16080, 16087, 16104, 16113, 16124, 16132 (fragment), 16152 (2), 16153, 16301, 16367, 16437, 17246, 17318, 17453, 17476, 17638, 17702, 18115, 18175, 18299, 18331, 18345, 18798, 18993, 19067, 19142, 19682, 20893, 20989, 21373, 21701, 22193, 22492, 23927, 24465, 24579 (3), 16910 (2), 27293, 27430, 27637, 28251, 30561, 30856, 31119, 31273 (3), 32475, 32885, 33049, 33766, 35991, 36618, 36882, 37296, 38000, 39671, 43420 (2) (articulated), 43707 (2), 44056 (2), 44684, 44766, 44804, 45761, 46175, 46205, 46326, 47041, 48093, 49132 (fragment), 49557, 50706, 51060, 51381, 51434, 51563, 51903 (2), 51949 (6),

51953 (18), 52053, 52055, 52061 (10), 52066 (2), 52068 (2), 52073 (19), 52079 (2), 52085 [23 (2 fused)], 52087, 52089, 52091, 52097, 52099, 52102 (96), 52105 (3), 52109 (10), 52112 (8), 52118 (2), 52125 (7), 52130, 52135 (8), 52137, 52139, 52141, 52146, 52147, 52218 (217); PTV: 14154, 15461, 16152, 16521, 16966 (3), 17363, 17722, 18228, 20419, 21311, 22095, 22598, 23665, 23863, 25487, 26007 (2), 26024 (2), 26823, 27090, 27352, 28240, 30922, 32114, 32720, 32885, 33259, 35897, 41625 (2), 43707, 45535, 45654, 46043, 48191, 51205, 51460, 51903, 51930, 51949 (2), 51953 (7), 52053, 52054, 52061 (2), 52066 (2), 52073 (3), 52075, 52085 (9), 52087, 52094, 52102 (35), 52104 (3), 52109 (4), 52112 (7), 52117, 52121, 52130, 52135 (4), 52142, 52146, 52157, 52161, 52199 (6), 52205, 52207, 52218 (68).

COMPARISONS. Dentigerous bones of *Thamnophis* usually have more alveoli per unit length than similar bones of colubrids (a notable exception is *Drymobius margaritiferus*). *Thamnophis* maxillae have medium-sized ectopterygoid and palatine processes and 21–25 alveoli. Anteriorly, the shaft of the bone curves strongly medially. The last two to three maxillary teeth are distinctly enlarged and compressed. *Thamnophis* maxillae lack diastemata.

Maxillae of *Drymobius margaritiferus* also have high tooth counts, and the last two to three teeth are also enlarged and compressed. However, these two genera differ in the shapes of their teeth and ectopterygoid processes. Teeth of *Thamnophis* are strongly recurved near the base, and the distal portion is straight or may even bend back ventrad near the tip, giving the tooth a slightly sinuous appearance. In addition, anterior maxillary teeth are as large as or larger than all but the posterior enlarged teeth. Teeth of *D. margaritiferus*, however, are smoothly recurved throughout and steadily decrease in size anteriorly. Finally, the caudal border of the ectopterygoid process of *Thamnophis* is approximately perpendicular to the shaft of the maxilla, whereas in *D. margaritiferus* this border is sloped strongly rostrally. *Nerodia* has maxillary tooth counts similar to those of *Thamnophis*, but *Nerodia* may usually be distinguished by its longer palatine and ectopterygoid processes that are not directed as sharply ventrad. Also, the ectopterygoid process of *Nerodia* is usually narrower and is roughly squared distally, whereas in *Thamnophis* this process is longer anteriorly, with a medial border that slopes toward the maxillary shaft.

The palatine of *Thamnophis* is elongate and has 14–16 alveoli. The choanal process is relatively broad and strongly recurved. The maxillary process is long, narrow, and rounded in cross section. The pterygoid process is usually strongly forked.

Lampropeltis and *Rhinocheilus* palatines have fewer teeth than those of *Thamnophis*. *Arizona*, *Coluber*, *Masticophis*, and *Pituophis* have choanal processes that are recurved only weakly or not at all. The maxillary process is shorter in *Arizona* and

Masticophis and flatter in *Coluber*. The palatine of *Drymobius margaritiferus* has more teeth (19) and lacks a forked pterygoid process. *Nerodia*, with similar alveolar counts, has a more curved choanal process that slopes toward the shaft. The choanal process is broader in *Thamnophis*, occupying four to four and one-half alveolar spaces, whereas in most *Nerodia* it occupies only three. Also, the maxillary process is larger and more posteriorly placed in *Nerodia*.

Pterygoids of *Thamnophis* have 20–34 alveoli ($n = 35$, 10 species). The alveoli extend nearly to the posterior end of the bone. The quadrate process is relatively short. The palatine process has a distinctive ventrolateral notch distally for the reception of the forked posterior end of the palatine.

Lampropeltis, *Masticophis*, *Nerodia*, *Rhinocheilus*, and *Salvadora* have longer, narrower quadrate processes. The pterygoid of *Coluber* is more constricted posterior to its ectopterygoid articulation. *Drymobius margaritiferus* does not have a distal notch on its palatine process.

The dentary of *Thamnophis* has 27–30 alveoli. Meckel's groove usually closes opposite the sixth alveolus. *Thamnophis* dentaries are distinguishable from those of most colubrids by the higher alveolar counts. *Drymobius margaritiferus*, with similar alveolar counts, may usually be distinguished by the fact that the distal end of its dentary is more strongly curved medially. Furthermore, the lateral notch for the compound bone is narrower in *D. margaritiferus*. Tooth shapes differ as described for the maxilla. In *Thamnophis*, the distal portion of the dentary narrows abruptly in the vicinity of the anterior end of Meckel's groove, whereas in *Nerodia* the dentary tapers smoothly throughout.

In *Thamnophis*, the prearticular crest of the compound bone is more elevated than the surangular crest and is relatively strongly arched. The supraangular foramen is located far rostrally, and the *M. adductor posterior: pars profundus* inserts on a pronounced ridge on the medial surface of the prearticular crest. This ridge runs from immediately below the quadrate condyle rostrad to the anterior edge of the prearticular crest. The ridge of insertion for the *M. adductor mandibulae externus superficialis* is poorly developed or absent.

The compound of *Pituophis* differs as described for that genus. In *Coluber*, *Masticophis*, and *Rhinocheilus*, the surangular and prearticular crests are roughly equal in height. *Lampropeltis getulus* has a narrower mandibular fossa than does *Thamnophis*. *Salvadora* has a distinctly shorter compound bone with a relatively higher surangular crest than does *Thamnophis*. *Arizona* has relatively shorter mandibular fossae and retroarticular processes than does *Thamnophis*. In *Drymobius margaritiferus* the compound differs from that of *Thamnophis* in that the supraangular foramen is not located as far rostrally, the mandibular fossa is shorter, and the ridge of insertion of the *M. adductor posterior: pars*

profundus is less pronounced, running more abruptly dorsad to intersect the middle of the prearticular crest. *Nerodia* has a stronger, more arched prearticular crest and a well developed ridge of insertion for the *M. adductor mandibulae externus superficialis*.

Vertebrae of *Thamnophis* have been described by Auffenberg (1963). Identification of various natricine genera has been discussed by Auffenberg (1963), Brattstrom (1967), Holman (1962, 1977a), and Meylan (1982). MTV of this speciose genus are variable but present some distinguishable patterns. MTV are generally elongate with strong subcentral ridges. Neural arches are moderately vaulted to moderately depressed with convex to nearly flat laminae. Epizygapophyseal spines are generally well developed. Zygapophyses are moderately to strongly divergent. The zygosphene is generally narrow, flat, or nearly flat dorsally, and its anterior edge is flat to crenate. The neural spine is of medium to low height but is usually characterized by distinctive anterior and posterior overhangs. Accessory processes are of variable length but are generally thick and blunt distally. The hypapophysis is short, strongly sigmoid ventrally, and caudally directed.

In the PTV, the hypapophysis is much shorter and more blunt than in the MTV. The notch between parapophysis and cotyle is large, and subcentral lymphatic fossae are weakly to strongly developed.

Seminatrix, *Storeria*, *Tropidoclonion*, and *Virginia* have elongate MTV, but have low to obsolete neural spines (Auffenberg, 1963). *Nerodia* and related genera usually have shorter vertebrae with higher, shorter neural spines.

ALLOCATED MATERIAL. ATV: 17862, 20906, 21888, 24621, 49349, 52067, 52073, 52075 (2), 52079, 52085, 52087 (2), 52102 (6), 52109, 52112, 52117, 52135, 52138, 52160, 52182, 52199, 52205, 52218 (11); PCV: 16124, 24009, 26007, 30561, 50343, 52087, 52102 (2), 52109, 52155, 52218 (14); IATV: 14968, 51930 (2), 52209; IMTV: 14477, 14997, 15036, 16089, 16362, 25300, 40889, 43116, 51953, 52061 (4), 52066 (4), 52067 (3), 52075 (3), 52078, 52085 (8), 52087, 52094, 52102 (8), 52104 (5), 52109 (5), 52112 (2), 52125 (2), 52148, 52156, 52199, 52205, 52218 (21); IPTV: 29827, 50918, 51717, 52066, 52073 (2), 52075 (2), 52085 (4), 52087, 52109 (3), 52135, 52199; H: 30922, 52104, 52137, 52182 (3), 52199 (3).

COMPARISONS. The neural arch of the ATV is highly vaulted and has convex laminae. The neural canal is higher than wide. Epizygapophyseal spines are usually reduced. The neural spine is about as tall as in the MTV but is much shorter (anteroposteriorly). Accessory processes are very short, thick, and blunt. Hypapophyses are often slightly longer and may be slightly more to much more ventrally directed. They may be sharp to nearly squared ventrally.

The precloacal vertebrae of *Thamnophis* have

small cotyles and condyles. Their hypapophyses are short and thickened ventrally.

Vertebrae of immature *Thamnophis* may be somewhat shorter to much shorter than those of adults. Vertebrae of neonates tend to be quite similar in relative proportions among species. Most specific vertebral differentiation apparently occurs during postnatal ontogenesis. The condition of the neural arch in neonates is little different from that seen in adults except that the posterior notch is generally wider and more obtuse. Zygapophyses of neonatal *Thamnophis* are less divergent than those of adults. Neural spines are comparable in height but slightly to much shorter anteroposteriorly. Accessory processes are generally shorter and acutely pointed distally. Hypapophyses of neonates tend to be more spine-like, have simple anterior edges, are sharply pointed, and are directed strongly caudad.

DISCUSSION. *Thamnophis* is the only natricine genus presently found in the extreme southwestern United States (Stebbins, 1985). The referred remains are either too fragmentary to assign to species or fall within the range of overlap for *T. sirtalis* and the *T. couchii* group.

It is worthwhile to underscore here highly convergent morphologies of the dentigerous elements of *Thamnophis* and *Drymobius margaritiferus*. This convergence may reflect dietary similarities. Close comparisons of skull elements of these two genera and of the vertebrae of *Drymobius* with racers should be made when considering any ophidian paleofauna from the southwestern states or Central America. No other species of *Drymobius* were available for comparison.

Family VIPERIDAE Bonaparte, 1840

Subfamily CROTALINAE

Gray, 1825

Genus *Crotalus* Linnaeus, 1758

Crotalus viridis (Rafinesque, 1818)

REFERRED MATERIAL. Dentary: 52170; MTV: 14729 (2), 14974, 14975, 15014 (fragment), 17798, 17997, 18049, 20167, 22603, 27648, 29963, 29964, 30992 (fragment), 34702, 37476, 42121, 47848, 48486, 51127, 51906, 51942, 51963, 51967, 51968, 52119 [2 (1 fragmentary)], 52213 [3 (1 fragmentary)]; PTV: 10031, 14970, 15996, 22776, 43061, 49556 (fragment).

COMPARISONS. The dentary of *Crotalus* is easily distinguished from those of most other North American snakes. It is very deep and narrow with a gently curved distal tip. Its depth does not taper anteriorly until the third alveolus and then only slightly. Meckel's groove is usually open lingually to the distal tip, but in a few cases it is closed at the tip or is closed to a suture just posterior to the tip, only to reopen at the tip. A foramen is present on the lingual side distally.

Most colubrid species have dentaries that are not

as deep or taper gradually from the posterior to rostral end. Meckel's groove is variable but is never entirely open lingually to the tip. No other crotaline genus observed possesses a distal foramen on the lingual side.

The single fossil dentary falls within the range of variability of recent *Crotalus viridis* but should be considered a tentative assignment at the species level because of overlap of characters among species.

Crotalus vertebrae may be identified by characters given by Auffenberg (1963), Brattstrom (1964), and Holman (1965). *Crotalus* MTV are short to very short and broad. The neural arches are moderately to strongly depressed, with flat laminae. The neural canal is moderately depressed and, in anterior aspect, is usually wider ventrally than dorsally. Zygapophyses vary from moderately to extremely divergent. In large forms, the prezygapophyses may become elongate and subrectangular with the long axis laterally directed. Prezygapophyseal buttresses are very high. Cotyles and condyles are large. Neural spines vary from high to low, anterior overhangs are generally absent, and posterior overhangs may be present. Accessory processes are very short and generally acute or blunt. Subcentral ridges may vary from moderate to poorly developed. The hypapophysis is long, thick laterally, posteroventrally directed, and often sharply pointed distally.

Neural arches of *Crotalus* PTV may be slightly more depressed than those of MTV. Zygosphenes are crenulate anteriorly. Hypapophyses are shorter and more posteriorly directed. Subcentral lymphatic fossae tend to be weak or absent throughout most of the column. However, in the posterior portion of the PTV, fossae may be apparent ventrally between the parapophyses and the cotyle, creating a slight notch in anterior view and faint emargination of the ventrolateral edge of the cotyle.

Agkistrodon has larger fossae lateral to the cotyle than does *Crotalus*. These fossae usually have a single large foramen in *Agkistrodon*, whereas in *Crotalus* the foramina are smaller and may be multiple (Holman, 1963, 1965). *Sistrurus* has relatively longer centra and may have a small spine on the zygosphenes anterior to the neural spine (Holman, 1965).

These vertebrae are assigned to *Crotalus viridis* on the basis of the shape of their centra, which are relatively longer than in most other *Crotalus* species, and their relatively low neural spines. MTV of *C. atrox* Baird and Girard, 1853, *C. molossus* Baird and Girard, 1853, and *C. ruber* Cope, 1892 have shorter centra and higher neural spines. The centra of MTV in *C. mitchelli* (Cope, 1861) are somewhat shorter, and their neural spines are lower. *Crotalus scutulatus* (Kennicott, 1861) has higher neural spines. *Crotalus cerastes* Hallowell, 1854 MTV differ in that they have wide, dorsally convex zygosphenes.

ALLOCATED MATERIAL. ATV: 31086, 41014,

51955, 52119; IMTV: 52110, 52134 (2), 52201, 52213 (2); H: 41327.

COMPARISONS. ATV in *Crotalus* have about the same relative length as MTV. Neural arches of ATV are slightly more vaulted with slightly convex laminae. Zygapophyses are much less divergent than those of the MTV. Accessory processes are extremely short and sharply pointed. Hypapophyses of ATV are extremely long, thinner than in MTV, and ventrally directed.

Vertebrae of immature *Crotalus* are only slightly shortened relative to those of adults. Zygapophyses are less divergent, and their facets tend to be rounded. Accessory processes are short but thin and pointed. Cotyles and condyles of immatures tend to be flattened dorsally and slightly drawn out ventrally imparting a subtriangular shape.

DISCUSSION. This species is known from a wide variety of habitats, including coastal sand dunes, wooded regions, near water courses, and prairies, but is not known from desert regions. *Crotalus viridis* occurs in the Los Angeles area today (Stebbins, 1985).

Crotalus viridis was reported from Rancho La Brea by Brattstrom (1953b, 1958). Other Rancholabrean records of this species from California include the McKittrick Asphalt deposit, Hawver Cave (Brattstrom, 1953a), Mescal Cave (Brattstrom, 1958), and Costeau Pit and Newport Beach Mesa (Hudson and Brattstrom, 1977).

CONCLUSIONS

Eight modern snake taxa are added to the known herpetofauna from Rancho La Brea, increasing the number of recognized snake species from four to 12. Newly reported taxa are *Diadophis punctatus*, *Hypsiglena torquata*, *Tantilla* sp., *Arizona elegans*, *Masticophis lateralis*, *Rhinocheilus lecontei*, *Thamnophis couchii* species group, and *T. sirtalis*. Of these, *M. lateralis* and the *T. couchii* group have not previously been reported as fossils.

FAUNAL COMPOSITION AND LOCAL PALEOENVIRONMENT

The composition of the Pit 91 snake fauna suggests that the local paleoenvironment probably included a stream and associated riparian woodland. Other habitats in the vicinity may have included chaparral, sage scrub, and/or patches of open grassland. These reconstructions are based on the relative abundance of fossil taxa (Table 1) and the habitat preferences of the living species (Table 2). The reconstructions are corroborated by geological and paleobotanical evidence (Woodard and Marcus, 1973; Warter, 1976; Shaw and Quinn, 1986).

The relative abundance of a taxon is represented by the percentage of the total number of identified specimens (NISP) for that taxon in the assemblage (Table 1). NISP is used because of difficulties inherent in determining the preferable minimum number of individuals (MNI) in snake assemblages

Table 1. Numbers of identified specimens (NISP) of snake species from Pit 91. Taxon names are abbreviated with first two letters of genus and first letter of species name.

Skeletal elements*	Snake taxa†													
	Ar.e	Co.c	Co.-Ma.	Di.p	Hy.t	La.g	Ma.l	Pi.m	Rh.l	Ta.sp	Th.c	Th.s	Th.sp	Cr.v
VT	5	56	58	66	30	25	10	145	4	10	39	7	936	50
MX	0	1	0	1	0	1	0	3	0	0	0	0	5	0
DN	0	0	0	0	0	0	0	0	0	0	0	0	2	1
CP	0	1	0	1	0	0	0	1	0	0	0	0	1	0
PT	0	0	0	0	0	0	0	1	0	0	0	0	1	0
PL	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Total NISP	5	58	58	68	30	26	10	150	4	10	39	7	946	51
Percent NISP	0.3	3.8	3.8	4.5	2.1	1.8	0.7	9.9	0.3	0.7	2.7	0.5	64.0	3.4

* VT = vertebrae, MX = maxilla, DN = dentary, CP = compound bone, PT = pterygoid, PL = palatine.

† *Arizona elegans*, *Coluber constrictor*, *Coluber-Masticophis*, *Diadophis punctatus*, *Hypsiglena torquata*, *Lampropeltis getulus*, *Masticophis lateralis*, *Pituophis melanoleucus*, *Rhinocheilus lecontei*, *Tantilla* sp., *Thamnophis couchii* species group, *Thamnophis sirtalis*, *Thamnophis* sp., *Crotalus viridis*.

(Meylan, 1982). Abundance of skeletal elements in fossil assemblages depends on two major factors: (1) the species' densities in the local environment and (2) the proximity of the populations to the depositional environment (Shotwell, 1955). A third factor, the number of elements per individual, may be important because the number of body segments is variable even among lower-level taxa.

The abundance of each taxon in conjunction with its presently preferred habitats (Table 2) gives a crude indication of paleohabitat and its proximity to the site. Moreover, skull and juvenile elements are thought to represent a population near the site of deposition because of their fragile nature and greater probability of destruction if subjected to transport.

The genus *Thamnophis*, which accounts for more than 67% of the identifiable assemblage (Table 1), suggests that there may have been an aquatic habitat near the site. Most members of the *T. couchii* group are semiaquatic and feed on amphibian larvae and fish. The presence of the *T. couchii* group suggests that there was a permanent or semipermanent body of water. *Thamnophis sirtalis* suggests mesic areas. *Diadophis punctatus* inhabits relatively moist fields and woodlands (Table 2). Stream and overbank deposits in stratigraphic section (Shaw and Quinn, 1986) confirm the inference that the site was located at or near a stream with associated riparian woodland.

Four other species are well represented (Table 1) in the Pit 91 assemblage: *Pituophis melanoleucus*, *Crotalus viridis*, *Coluber constrictor*, and *Lampropeltis getulus*. These may be found today in a wide variety of habitats, but are most characteristic of chaparral and grassland associations in the western United States. The remaining species, accounting for only about 2% of the NISP (Table 1), are characteristic of semiarid or arid habitats, ranging from desert through chaparral and prairies. Their low

abundance suggests either low population sizes in the immediate vicinity or that an occasional specimen found its way into the deposit from neighboring habitats. Some of these remains are abraded, which could indicate allochthonous origins, such as via stream transport. Also, a riparian woodland would provide ideal roosting and nesting sites for raptors that might forage in nearby open country.

The paleoenvironment in the region of Pit 91 appears to have consisted of two habitat components: (1) a moist riparian area near the site of deposition, inferred from the abundance of *Thamnophis* remains and the presence of stream deposits, and (2) a distal semiarid habitat, perhaps similar to modern chaparral or coastal sage associations, inferred from the presence of small numbers of *Arizona elegans*, *Masticophis lateralis*, and *Rhinocheilus lecontei*. Warter (1976) gives a detailed account of the flora of Pit 91. Her interpretations generally agree with those presented here.

It is noteworthy that the semiaquatic and mesic habitat snakes contributed the highest percentage of NISP and the lowest diversity (i.e., the *T. couchii* group, *T. sirtalis*, and *Diadophis punctatus*). Remains identified to only generic level (*Thamnophis* sp.) probably represent one or both of the above forms. Conversely, the species that prefer semiarid habitats are more diverse. This suggests that the riparian habitat was somewhat isolated within a more extensive semiarid region, a condition similar to the historic environment of the Los Angeles region. The presence of a permanent water source indicates a slightly moister climate, as suggested by Brattstrom (1953b).

EXTINCTIONS AND HABITAT REQUIREMENTS OF REPTILES AND AMPHIBIANS

Very few extinctions appear to have occurred among North American reptile or amphibian species at the

Table 2. Habitat preferences of the Pit 91 snakes, based on the relative abundance of modern species in that habitat. Species names are abbreviated with the first two letters of the genus and the first letter of the species name.

Habitats*	Snake species†											
	Th.c	Th.s	Di.p	Pi.m	La.g	Cr.v	Co.c	Hy.t	T.sp	Ar.e	Rh.l	Ma.l
FW	H‡	I	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne	Ne
RW	I	H	H	I	I	I	I	L	L	I	L	L
F	Ne	L	I	I	I	I	L	Ne	Ne	L	Ne	L
G	Ne	L	I	H	H	H	H	I	I	H	H	I
C	Ne	L	I	H	H	H	I	H	H	H	H	H
X	Ne	Ne	Ne	I	I	L	L	H	H	H	H	I

* FW = freshwater semiaquatic, RW = riparian woodland, F = forest, G = grassland, C = chaparral, X = xeric.
† *Thamnophis couchii*, *Thamnophis sirtalis*, *Diadophis punctatus*, *Pituophis melanoleucus*, *Lampropeltis getulus*, *Crotalus viridis*, *Coluber constrictor*, *Hypsiglena torquata*, *Tantilla* sp., *Arizona elegans*, *Rhinocheilus lecontei*, *Masticophis lateralis*.
‡ H = highest abundance, I = intermediate, L = lowest abundance, Ne = not expected.

end of the Pleistocene, in marked contrast to the many extinctions that occurred among large birds (Welty, 1975) and large mammals (Kurten and Anderson, 1980) at that time. About 14% of the avian species (Howard, 1962) and 39% of the mammalian species from Rancho La Brea are extinct (Stock, 1956; Akersten *et al.*, 1979). Nearly all of the extinct mammals were larger than a hare. The extinct birds were mainly large raptors and carrion eating forms. Megafaunal extinctions can be accounted for by the overkill hypothesis of Martin (1967, 1984). However, the actual impact of paleoindian hunters is not known with certainty, and the hypothesis competes with many other ecological and climatic models. One thing is certain, terminal Pleistocene events had very different effects on large mammals, small mammals, and reptiles. Eagerness to embrace the overkill hypothesis should not be allowed to obscure other factors that may have influenced the composition of the modern fauna.

Guilday (1967) argues convincingly that large mammals will disappear first during periods of rapidly changing climate in which critical habitats are reduced to small refugia or extirpated. Extinction of large scavenging birds that depended on the mammalian megafauna would naturally follow. Small mammals throughout the United States are known to have experienced substantial range fluctuations and to have occurred in faunal assemblages that are considered ecologically incompatible by modern standards (Fay, 1988). Thus, although few small mammal species went extinct at the end of the Pleistocene, they were obviously affected by the climatic changes that occurred but to a lesser extent than the megafauna (Martin, 1967, 1984).

If fluctuating resource levels and habitat size contributed to the alteration of the endothermic fauna seen in the terminal Pleistocene, the low resource requirements of small ectotherms suggests that they will be the last species to be affected by these forces. Pough (1983) and Regal (1983) characterize amphibians and reptiles, and lizards, respectively, as

components of low energy-flux systems. Many reptiles and amphibians specialize in low productivity habitats, such as deserts, that are considered sub-optimal or harsh for endothermic species. Furthermore, metabolic rates of ectothermic species are usually modulated by changing weather conditions such that annual periods of inhospitable weather can be readily accommodated, as during aestivation. Thus, trends toward increasing aridity (Van Devender and Spaulding, 1979) and seasonality (Graham and Lundelius, 1984; Guthrie, 1984) during late Pleistocene and early Holocene times probably favored many reptiles by increasing the areas that they could exploit more effectively than could endothermic competitors. In addition, low resource requirements per individual may allow ectotherms to maintain viable populations in small refugia with insufficient area (hence resources) to support viable populations of similar-sized endotherms, let alone megafauna.

If this hypothesis is true, then there may be a basic dichotomy between endothermic and ectothermic faunas in the rate of change in their species compositions. Faunal turnover would be much more rapid among endotherms, whereas ectotherms would have greater species longevities. If extant species of mammals and reptiles are followed backward through time via literature records on fossil occurrences, it is readily observed that the origins of extant mammal species are much nearer the present than are the origins of extant reptile species. In fact, most mammal species that are represented in the fossil record appear to span shorter time intervals than do reptile species (LaDuke, 1987).

Thus, it is probably no coincidence that when terrestrial mammals and reptiles are considered together, the amount of biological disruption experienced by each species (i.e., extinction, morphological change, and range modification) at the end of the Pleistocene appears to be correlated with the absolute quantity of resource requirements of individuals of that species.

Giant tortoises (*Geochelone*) are not ecologically comparable to other North American reptiles because of their large size and herbivorous habits. They regularly require large masses of vegetation for maintenance and growth. Thus, their resource requirements may be more comparable to those of a medium-sized endotherm. Hibbard (1960) suggested that these tortoises went extinct in North America as a direct result of physical rather than biotic influences (i.e., low winter temperatures coupled with the inability to hibernate). It is also known that paleoindians preyed on at least one giant tortoise (Clausen et al., 1979).

Fay (1984, 1986, 1988) suggests an alternative to the above model. Amphibians and reptiles may be capable of acclimating to climatic change more readily than mammals. This would also produce the pattern above but does not exclude the resource hypothesis. The two phenomena acting in concert would accentuate the pattern of increased span of species life. These various hypotheses are representative of a field of study rife with opportunities for further research.

Alternatively, the pattern of more gradual change exhibited by ectotherms could have been produced by an inability of paleontologists to discern species with the precision that is often achieved with mammals. Paleoherpetologists must often use elements that are less reliable than the morphologically labile mammalian teeth in making identifications. Thus, we might expect amphibians and reptiles to have a greater apparent species longevity. Carefully controlled quantitative studies of biometric variability in living and fossil reptiles may help to resolve these issues.

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